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NEW EXPERIMENTS ON THE LIGHT REACTIONS OF PLANTS AND ANIMALS:

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T

Gentlemen: Allow me, before the order of the day, to give a brief report of a discovery, which, though it stands only in loose relation to our theme, seems to me of general interest. I speak of the accommodation of the alciopids.

The alciopid is, as you know, a nearly transparent pelagic annelid, whose comparatively highly developed eyes have been repeatedly the object of histological research. It was believed that muscular elements could be demonstrated anatomically in these eyes and on this supposition theories of the act of accommodation were grounded. These theories can easily be proved mistaken, as the following shows; I will not further dwell on them.

On account of the small size of the eyes the largest—which I was enabled to examine had a diameter of hardly 1 mm.,—it had been considered heretofore impossible to attack the problem of their accommodative changes experimentally.

However, I was able, by laying the living and carefully isolated eyes on suitable electrodes, under seawater, and by observing them through binocular lenses in a very strong light falling from above, to follow the changes caused by electric irritation, and thus to discover a most remarkable accommodative process, unique in the animal world.

At another time I shall describe this process in detail, tonight I shall limit my description to the main facts.

¹ A lecture before the Morphological Society of Munich, reported and translated by Miss Hilda Lodeman.

If one views a fresh alciopid eye from in front, the surface surrounding the lens is seen to be threaded over with numerous fine silvery shining stripes, which have hitherto been mistakenly interpreted as muscles (Hesse). In fact these are structures which, like an iris, obstruct the passage of diffuse light into the eye; besides this, they make the eyes which are turned forward and downward, as invisible as possible to an enemy coming from below. They thus have the same effect as that which I some time ago proved to be the case with the silver sheen of fish.

Just below the lens there is a spot in the very soft eye-wall which, one may observe, contracts when the eye is stimulated: all the other portions of the tegument remain motionless. The lens, when stimulated, moves forward perceptibly, it approaches the cornea, as one may perceive most readily by looking at the eye in profile. Herewith is proved that the alciopids have an active near accommodation; for, by the above-mentioned contraction the distance between the lens and the retina is increased, while the lens remains unchanged in form. The way in which the change in the location of the lens is brought about is most interesting: The alciopids are distinguished from all other animals with otherwise similarly constructed eyes, by possessing a double vitreous body. Directly back of the lens we find a viscous fluid which is distinctly separated from the posterior space of the vitreous body and adheres closely to the walls of the eve on all sides. At the lowest point of this front part of the vitreous body the latter displays a curious ampulliform knob which is connected with the eye-water space by a canal and was formerly interpreted as an auditory sac by zoologists, and at present is supposed to be a gland belonging to the vitreous body for the secretion of its substance. My experiments show the real use of this protuberance. It occupies exactly the spot in the eyewall in which alone contractile elements are found; the muscles, contracted, press the lump together like a rubber bulb filled with liquid, thus forcing a part of its contents into the eye, and slightly pushing forward the lens which rests in a bowl-like groove in the front surface of the vitreous body.

This is the second accommodative process among the invertebrates with which we have become acquainted; the mechanism differs entirely from that which I have proved Cephalopods to

possess. Our observations teach anew how greatly physiological experiment can aid us in the interpretation of histological discoveries.

Π

Among the lightreactions of Echinodermata which I have newly discovered and upon which I shall make only a brief report tonight, a certain interest attaches to those of the star-fish, if for no other reason but that until now almost nothing of their sensitiveness to light was known. On the ground of anatomical research it was taken for granted that the familiar red points at the ends of their five arms were light receiving apparatus. Attempts to elucidate the question experimentally led to contradictory results. Some authors assert that those starfish which have an inclination to move toward the light cease showing this impulse after the tips of the arms with the "eyes" are cut off; according to other writers individuals thus mutilated still crawl to the light.

In the course of systematic experiments I discovered the surprising fact that the feet of the Astropectinids are highly sensitive to light. If light is flashed on them their little feet, relaxed in the dark, are instantaneously jerked in and the widely opened ambulacral groove is closed along the whole of the lighted area, the flanking white spines shutting over the incurled little feet. This startling phenomenon, which I was able to record in a number of snapshots, gave me the opportunity of examining the differing effects of colored lights. As with all the hitherto thoroughly examined invertebrates, it was found that colored lights have similar or identical relative values for our starfish as for the totally color-blind human eve; red lights remain almost or quite without effect even when very strong, while green and blue lights have a much stronger effect than the red lights, even when the latter seem to our normal eyesight much darker than the former. I was able also to prove adaptive changes in these starfish and to carry out exact measurements during my observations.

New and most remarkable light reactions in sea urchins were also disclosed. So far it had been known from experiments of Sarasin and Uexkull that some sea urchins raise their spine slightly when shaded from the light. More exact observations of their qualities of sight had not yet been made. I discovered

the following interesting phenomenon appertaining to Centrostephanus longispinus. The animals have surrounding their aboral pole, 20 or 30 beautiful lilac colored, clublike processes about 3 mm. long, concerning which we knew hitherto only that they sometimes move in rotation, at other times are quiescent. I noticed that if a specimen at rest was slightly shaded, for example, if one's hand were passed quickly between window and reservoir, the little clubs began to rotate in a most lively manner. Further experiment showed that in order to bring about such agitation an exceedingly slight lessening of the lighting suffices. If, for instance, the greater part of the light reaches the animal from a gray pasteboard held at the proper angle, and I replace this board with one which is only a little darker in shade, the clubs begin to rotate quickly. Even with this method it was possible to a certain degree to make determining measurements, and I was able by the further use of differently colored boards for the lighting again to show convincingly that these animals also behave like totally color-blind human beings brought under corresponding conditions. Still more delicate, surprisingly exact measurements were made by using the method which I shall now describe.

III

Several writers have thought to deduce an argument against the experiments I have so far made with the qualities of sight in animals from the idea that I bring the "objective light-reaction" of animals into relation with the "subjective light sensation" of man. For anyone to whom the science of color is familiar, this argument is easily controverted. Still it is evident that there is a great advantage in showing that the problem may be attacked from quite a new direction. Therefore in a new series of experiments on a large scale, I brought the light sensitiveness of animals into relation, not to the "subjective light sensation" of human beings, but to the "objective light reaction" in the human eye, to the changes in the size of the pupil caused by light. This correlation was successful after I had made extended and rather difficult preparations, as follows:

We know from former experiments of M. Sachs (1893) that the degree of contraction of the pupil caused by a colored light, the "motor irritative value" of a colored light, depends on the strength of luminosity in which the colored light is seen. Until now we lacked a practical method of comparing the changing

size of the human pupil and the varying reactions to light in the lower animals. Here you see an apparatus² which I constructed for this purpose and which does excellent service also in examining physiological and pathological changes in the human pupil. Of this use of the instrument I shall speak elsewhere in detail. At present it shall be described only in so far as it serves in the solution of the problems in comparative physiology now before us. With the aid of a proper system of lenses. and placed at a certain distance from it, a Nernst lamp illumines very strongly and evenly a circular space. In front of the first lens there is a movable double frame which by a lever arrangement enables one to light this circular space first by a physically exactly determined colored glass light, and immediately thereafter, without intermediate lighting, by a mensurable variable light of almost colorless gray, for comparison. The change in the strength of light in the gray field is caused by the sliding in opposite directions of two acute-angled prisms of gray glass. For every position of the latter, the amount of light which penetrates it from the Nernst lamp is determined; this amount will be expressed in the following table in percentages of the strength of the Nernst light. With this apparatus, which can be used for many purposes, I have made a large number of measurements; if I give only a brief summary of these, please do not conclude a correspondingly brief period of labor on this subject: the table below is alone the result of over 1.000 separate measurements.

MOTOR IRRITANT VALUES OF COLORED-GLASS LIGHTS

The numbers give the amount of light allowed to fall through the gray prisms in percentages of the whole amount striking these, the motor equation determining the former amount.

Normal human being	Relatively color-blind blind for red and green, out seeing blue)	Fotally color-blind	Oove	Night bird	Sepia	Sees	Centrostephanus	Sammobia
4	R-D	T	Н	4	00	124	0	14
9-11 1.5-2.5	1.5-2.2 2-3	<0.6 9.9-11.8	7.3-9.3 0.8-0.9	0.9-1.1 7.4-8.8	<0.6 9.3-11.1	<0.6 8.3-11.1	<0.8 11.1-14.8	<1.0 8.3-14.8

² This apparatus, "Differential Pupilloscope," is manufactured by C. Zeiss.

Red

I began with measurements of the normal human eye in order to determine the average pupillomotor irritant value of the various colored lights. Further measurements of relatively blueseeing, red-green blind (so-called red-blind), showed, as may be seen in the table, that a very slight irritant value of red, and a hardly perceptible variation from the normal motor-irritant value of blue, are characteristic of this disturbance of the sense of For the sake of brevity I shall limit myself in the following to the discussion of the red and blue values, these being of the greatest importance to us. In two cases of totally colorblind which I have repeatedly examined, red proved to have a very slight motor-reactive value (<0.6), blue, a comparatively high value of 9-11.8% (as compared to 1.5-2.5% in the normal eye). These are the three principal kinds of pupil reactions which occur among normal and color-blind human beings and with these we must compare the motor reactive values found among the different animals.

For the day bird, the sensitive value of red is like our own; this corresponds to the fact which I had already discovered by another method, that day birds in most cases see red lights nearly or quite as we see them. The relatively small values of blue,—they are the smallest which I have met with in the animal series—correspond to another fact which I had discovered, namely, that day birds in consequence of red and yellow oil globules located in front of the light receiving ap-

paratus, are relatively blue blind.

With the help of the apparatus I was enabled, among other things, to answer the following question, which I raised some time ago. The beautiful blue of the feathers of many birds is interpreted by almost all zoologists as decorative color for the attraction of the other sex: this interpretation assumes that these birds see blue as we see it, that therefore the oil drops do not exist. For if these drops are found in the eyes of these birds as they are found in the hen and the dove, then a blue which seems to us gorgeous must look to them blue-gray or colorless gray. So far I have had no opportunity to examine such birds with the spectrum according to the method described; but a short time ago I examined the movements of the pupil of the Butterfly-finch (Mariposa phoenicotis) with the new apparatus; the motor values are the same as for chicken and dove:

and herewith it is proved that the beautiful blue on breast and tail of this bird cannot be for adornment.

Among the night birds I found the motor values like those of the color blind human eye, a fact which corresponds to the superior number of rods and cones in the retina of these birds. The relatively slight differences are sufficiently explained by the fact that in the retina of the night birds, the cones are not entirely lacking as many assume; indeed, I have repeatedly been able to count in such retinas one to two million cones, with slightly colored oil balls.

Among the invertebrates, examination with the new apparatus of the movements of the pupils of Cephalopods, which are particularly well suited to the measuring experiments, shows as you see striking conformity to the irritative values for the totally color-blind human eye. By the use of other methods also, I have been able to show that these invertebrates are totally color-blind. I cannot here dwell on these new experiments.

A glance at the table will show you further that the motor-sensitiveness of bees to colored lights, of mollusks (*Psammobia*) and of sea urchins (*Centrostephanus*) is almost identical with that of a color-blind man, whereas it differs characteristically from that of red-blind eyes. The reaction of bees I need not mention again, as the bees as well as fish and crabs may easily be proved totally color-blind by other methods which I have developed. The continually repeated mistaken assertions of a few zoologists, from which a color sense in these animals is supposed to be deducible, need no new refutation after the above measurements are studied by anyone at all familiar with the subject.

The advantages of the new methods of research which I have here briefly indicated consist essentially in the following points: All the light reactions which I have hitherto carefully investigated in animals, the contraction of the pupils in birds and invertebrates, the swimming of fish and crabs and the flying of bees toward the light, the phenomena of retraction in Serpula and Psammobia, the rotations of the little clubs in the Centrostephanus, etc., all these manifold movements which are caused by increasing or lessening the light, we are able by the help of our apparatus to measure with the identical, physically exactly determined colored lights, and to express their motor-sensitive

values in terms of one and the same measurable variable light with which each colored light is compared. Besides this, we are now in a position to bring all these reactions of animals in relation to the motor-sensitive values which the same colored lights have for the pupil of the normal, the red-blind, and the totally color-blind human eve.

That it would be possible to carry out such exact measurements by this new process, I myself could not foresee at the beginning of these tests; as the results obtained coincide in every detail with those of my former widely differing experiments, they prove most satisfactorily the accuracy of the statements I have previously made about the sight qualities of animals.

IV

The long well-known fact that, on plants, red lights have comparatively slight, blue, on the contrary, strong heliotropic effect, that therefore in this respect there exists a certain similarity between the effect of colored lights on plants and on animals, gave J. Loeb occasion to accept the "Identity of animal and plant heliotropism." Some time ago, referring to older experiments made by Wiesner and to more recent ones by Blaauw, I had expressed doubts of this theory; as in spite of this. Loeb's followers have again energetically taken up the defence of the identity of the two tropisms, it seemed to me advisable to attack this interesting question with new methods. In order to settle it so that every possible objection should be met, both reactions must be studied under identical conditions, with the same colored lights, and especially in quantitative experiments. the same light for measuring must be used for both.

These conditions were fulfilled by the following procedure. Etiolated seedlings of various kinds, in long narrow boxes, were exposed on one side to the rays of a suitable Nernst-light spectrum and simultaneously from the opposite side, to the light used for measurement and comparison, the latter being variable. an electric light placed in a tunnel adapted to the purpose. Its strength I varied partly by changing its position as required, to distances nearer to or farther from the plants, and partly by means of an episkotister. This method proceeds in the same lines as those developed in my experiments with Artemia and other animals which shun the light. Starting from a medium

distance found by preliminary trials, after a very few hours we find the plants in red, vellow and green bent far over towards the measuring light, those in green, blue and a part of violet, towards the spectrum, those in the outer edge of violet and ultraviolet again bent toward the measuring light. Through this experiment we have found two lights in the spectrum whose heliotropic strength is equal to that of the composite light. The circumstance that the plants bend over on each side of these two colors in opposite directions make a comparatively exact spectroscopic determination of their respective wave lengths possible. By repeating such experiments, taking different distances of the lamp from the plants, I obtained each time two new points for the construction of curves. You see here the curve of the motor irritative values of the different lights of the spectrum for the invertebrates, next to it the curve of some among the plants (Brassica napus) which I have observed and you can see from these that there can be no question of identity between the two results; the curve for animals has its maximum in yellowgreen, with a wave length of about $526\mu\mu$, that for Brassica napus has its maximum in blue or in the beginning of violet, with a wave length of about $475\mu\mu$! In yellowish-green, where we find the maximum for animals, the heliotropic effect on the plants has already reached nearly its minimum.

A second method for the investigation of certain questions occupying my attention, I worked out in this way: I have already shown that one can obtain beautiful and convincing results if a reservoir is lighted by rays reflected from colored paper at both ends, and direct light from the window is shut off by placing shades as required. Animals seeking the light, without exception hasten to that end which is lightest in the opinion of a color-blind individual quite irrespective of the way in which normal sight interprets the values. The heliotropic movements of plants have hitherto been observed only when caused by light from the spectrum or through colored glasses; it had never been attempted to find out whether heliotropic movements appear also when light from such reflecting surfaces alone is used. After I had found in a few introductory experiments that such is in fact the case to a quite surprising degree, I used this method for the solution of the problem before us. is one easily adapted to the use of the interested layman.

If the tropisms were identical, the plants placed between the colored papers should behave in relation to these in exactly the same manner as animals under like conditions. If, however, the heliotropism of plants differs from that of animals as much as the curves indicate, then, if we carefully choose a green surface and a blue, place animals and plants between the two, the former will go to the green side and the plants will bend toward the blue in exactly opposite directions. This behavior is indeed quite marked as you see by the samples set before you. The plants bend over to the blue often in one to two hours after being placed in position.

I have taken the liberty of briefly introducing to you two new methods for the investigation of the heliotropism of plants, because I believe they may do good service in botanical experiments and elsewhere, especially in quantitative experiments, and because particularly the second method may easily be handled by amateurs, and gives marked results, besides being well suited to use in the lecture room. As to the pertinent scientific questions, these I have touched upon today only in so far as the often repeated assertions of Loeb, that animal and plant helio-

tropism is identical, required a final refutation.

V

In conclusion, let me add a word on my discoveries about the sight qualities of fish and invertebrates. Zoologists and botanists have again and again declared they cannot acknowledge my "theories" (as they call them) because they stand in too harsh contradiction to the prevailing doctrines. The truth of the matter is, that I have never set up any theory whatever, but have made known only facts which every conscientious observer may easily verify for himself. What Sprengel promulgated in 1793, and has been taught ever since about the connection between the coloring of flowers and the visits of insects, was a theory. This theory is now finally done away with, for it is built upon demonstrably wrong surmises as to the sight qualities of bees. Plant biology, for a hundred years and more under the ban of this doctrine, which even Darwin believed to be true, will now needs turn to the task of ascertaining the real meaning of the splendor of color in blossoms.

METHODS OF EXHIBITING REACTIVE TENDENCIES CHARACTERISTIC OF ONTOGENETIC AND PHYLOGENETIC STAGES

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Methods which have contributed importantly to our knowledge of the ontogeny and phylogeny of reactive tendencies, and more especially to those types of adaptive behavior which we call ideational, are few and unsatisfactory. Only recently have experimental devices and procedures been suggested which are alike suited to reveal the reactive tendencies of ontogenesis and phylogenesis and to stimulate interest in genetic description of behavior.

Following a brief historical sketch, I shall describe an apparatus by means of which three of the most recent and promising of our behavioristic methods may be used.

From the birth of interest in the problems of psychogenesis, about the middle of the last century, until the end of the century, no scientific means of approaching the problems of ideational behavior were developed. Romanes, Brehm, Morgan, and their psychological contemporaries who happened to be interested in evolutionary or genetic problems worked either from anecdotal materials or from observations gathered by the use of crude and unstandardized methods which may fairly be characterized as wholly unsuited to scientific inquiry. We regard their contributions to genetic psychology as suggestive of possibilities of research or as defining problems rather than as important additions to our knowledge of fact.

With the appearance of Thorndike's mental initiative, the situation radically changed, for the puzzle-box or problem method came into existence and began to be used systematically as a

¹ I shall designate as ideational behavior those forms of adaptive response which in objective characteristics are identical with, or strikingly resemble, what we appropriately and with common consent call ideational behavior in man.

means of testing for various types of behavior. Thorndike himself devised various forms of apparatus and problem, while at the same time making them contribute most stirringly to our knowledge of the psychology of the chick, cat, dog, and monkey. Kinnaman, Small, Porter, Watson, and a host of other American and European experimentalists followed Thorndike's lead in the application of experimental devices to the analysis of

problem-solving behavior.

It may not be amiss to point out that the puzzle-box method, although an important advance scientifically over the casually or inexactly arranged situations of the earlier period—not to mention the anecdote—does not adequately fulfill the requirements of comparative and statistical method. True, it has possibilities of adaptation or improvement in these respects which have never been realized, but the fact is that mostly the data of response to a puzzle-box problem or situation are so meager and inexact as to be of scant value for purposes of comparison or statistical treatment. Comparative and genetic psychology alike demand methods which shall yield precise, varied, and comparable data of reaction from measurements of various stages, types, and conditions of organization.

L. W. Cole departed from the well-worn path which Thorn-dike had earlier broken, in originating the serial stimulus method of testing for imaginal or ideational behavior. This method, also, was ill-adapted to statistical needs, and like the earlier procedures, yielded only roughly comparable data. As thus far used, it is an indicator of problems rather than a scientifically exact instrument for solving them or of obtaining detailed descriptions of behavior. It has already served an important end in breaking up the monotonous succession of problem-box

studies.

Simultaneously with Cole's work on raccoons, which really revived interest in animal ideation, Hamilton, from a very different direction, attacked the general problem of reactive tendencies. As a psychiatrist, he had become deeply interested in applying the comparative method to the problems of psychiatry and in bringing the facts of animal psychology and genetic psychology to bear upon the practical problems of mental disease and defect. His first experimental attempt was a study of reactive tendencies in the dog. Over a period of ten years, he has

gradually perfected his method, the while applying it to various ontogenetic stages in man, cat, dog, and monkey, to defective and deranged human adults, and to many and diverse types of animal.

The Hamilton method, which, in the opinion of the writer, is equal in importance to any method of studying behavior yet proposed, has been almost wholly neglected by comparative psychologists and its results are very imperfectly known.

While Cole and Hamilton were busy with their new methods, Carr and Hunter² were perfecting, in the study of the white rat, what has appropriately been termed the method of delayed reaction. It is a simple and ingenious way of testing for ideation. Like Hamilton's, Hunter's contribution to our science is important methodologically as well as for its factual materials. But whereas Hamilton's method of quadruple choices is suited to reveal reactive tendencies and to exhibit their genetic relations, Hunter's serves primarily as a test of the ability of an organism to respond to a situation from which the significant feature (stimulus) has vanished.

For purposes apparently foreign to the interests of both Hamilton and Hunter, the writer a few years ago devised yet another method of studying ideational and other reactive tendencies. It has been called the method of multiple choices. It was planned as a means of gathering strictly comparable data of reaction from diverse types of organism, stages of development, and conditions of normality or abnormality. It was the writer's hope and conviction that most varied scientific materials should be assembled systematically in the interest of genetic description. The method is therefore appropriate to human psychology and to infrahuman, to child psychology and to psychopathology.

To sum up:—for reasons which are obvious to every careful student of behavioristic method and result, Hamilton's method of quadruple choices is a preëminently valuable means of displaying reactive tendencies; Hunter's is an uniquely serviceable test of ability to respond appropriately to controllable absent stimuli; and the writer's is a promising mode of evoking varied types of response and of reactive tendency for purposes of classification and more detailed analysis.

² The method is hereafter referred to as Hunter's because he alone has published concerning it.

The three methods differ so much in value, or rather in their special kinds of serviceableness, that they may not be directly compared. All are useful in the study of ideational and other highly adaptive forms of behavior, but each has certain peculiar advantages, whatever the ideational problem in question. For this reason, chiefly, it has seemed to the writer important, as a matter of economy and efficiency of research, to devise a form of apparatus which should enable the investigator to use at will any one of the three methods.

It has not been especially difficult to plan such an apparatus, for the writer has had opportunity to use, and to see used, each method, and has had full advantage of the published results of Hamilton and Hunter, as well as personal contact with them. It may be convenient to refer to the device now to be described as the convertible ideational or reactive tendency apparatus. It is called an ideation apparatus, not because its usefulness is limited to the study of the function of the idea, but because it was originally devised as a means of discovering those types of behavior which are either definitely ideational or closely akin thereto. Objectivists who are offended by the term ideation may substitute reactive tendency or some other equivalent term.

The three methods for which this apparatus may be employed are presented, not as the final word in the study of complex behavior, but rather as the first words concerning a new approach to genetic problems.

DESCRIPTION OF APPARATUS

The apparatus consists (1) of twelve identical boxes, each with an entrance door and an exit door that can be raised or lowered by the experimenter from his observation stand; (2) a reaction chamber in which the subject responds, as may be, to a definite experimental situation, which may be described as a "setting" of the various mechanisms (this setting differs for the three methods, and also from trial to trial in the Yerkes' method); (3) a release box in which the subject is confined between trials and from which it is admitted, at the proper moment, to the reaction chamber; (4) alleys for the passage of the subject from the rear of the reaction mechanisms or boxes to the release box; (5) twelve reward mechanisms, one for each box; (6) a keyboard, or series of levers, (depending upon the size of

the apparatus) connected by means of cords or wires with the various entrance and exit doors of the apparatus, and so arranged as to enable the experimenter to unlock and open or to close and lock any given door by a simple movement of a key or lever; (7) a protected incandescent lamp in each of the boxes, with the necessary switch and timing mechanisms for its satisfactory use in connection with the Hunter method of delayed reaction (lamps need not be installed in the twelve boxes, but only in those which are to be used for the delayed reaction method).

This apparatus may be built in three sizes: small, medium, and large.

The small apparatus is suitable for experiments with such organisms as the toad, frog, lizard, tortoise, mouse, rat, sparrow, canary, and other like-sized amphibians, reptiles, birds, or mammals. The medium-sized apparatus is suited for experiments with the tortoise (large), snake, dove, crow, domestic fowl, cat, small dog, raccoon, rabbit, squirrel, marmoset, and other medium-sized reptiles, birds, or mammals. The large apparatus may be used for various types of large-sized lower vertebrates, and for such mammals as the cat (large), dog, pig, goat, sheep, bear, monkey, ape, and man.

The several figures indicate the general plan of the apparatus and certain of the most important points of construction.

Each reaction box, according to figures 1 and 3, and also according to the measurements of table 1, occupies five degrees of arc. The width of the box is therefore determined by its distance from the center X (figures 1 and 3). By making the boxes intercept six degrees instead of five, the advantage can be gained of shorter distances between release door and entrance door, but there results the serious disadvantage that the apparatus is so spread out as to demand a considerable eye movement for inspection of the twelve reaction boxes. There is the further disadvantage, in the wider angle, that the large apparatus requires for its installation a floor area of nearly thirty-six by thirty-six feet. For these and other reasons, it has seemed desirable to make use of the five degree angle in the designing of this convertible apparatus.

The alleys are, in each size of apparatus and throughout their lengths, the same width inside as the reaction boxes are outside.

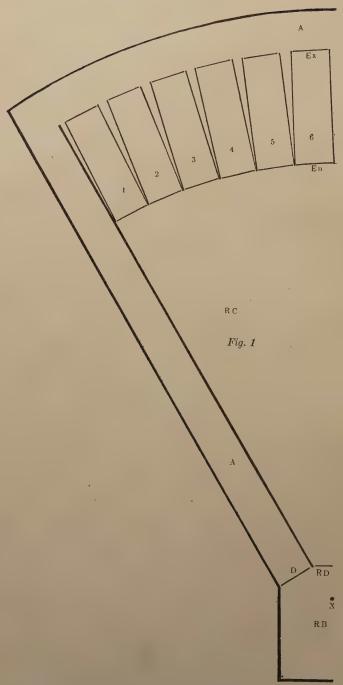


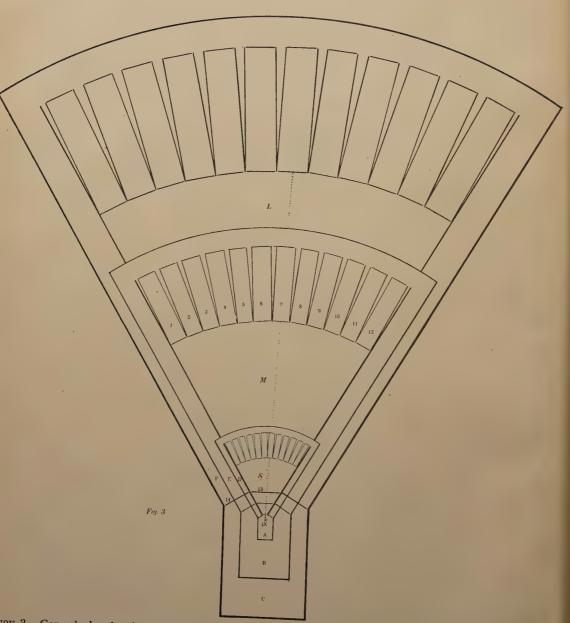
FIGURE 1.—Left half of medium sized reactive tendency apparatus. (1) 1-6, reaction mechanisms or boxes; En, entrance door; Ex, exit door; (2) RC, reaction chamber; (3) RB, release box; RD, door between release box and reaction chamber; (4) A, A, alley from reaction boxes to release box; D, door between alley A and release box; X, center of circle on arc of which reaction boxes are placed.

The plan of the medium sized apparatus appears as figure 1, and in figure 2 there is shown an enlargement of one of the reaction boxes, with the arrangement of sliding entrance and exit doors and the concealed reward mechanism. Figure 3 represents the three sizes of apparatus in their relations. These must, of course, be built separately and be independent of one another.



FIGURE 2.—Ground plan of reaction box. En, entrance door; Ex, exit door; s, s, wooden guides for sliding door; B, wooden block for food cup; R, food cup.

The small apparatus should be made of quarter inch white wood (poplar), red wood, or pine, according to locality, and covered with netting made of No. 20 wire, three meshes to the inch. The medium sized apparatus should be made of half inch stock, and the wire netting used as a covering, or for other necessary purposes in connection with it, should be No. 17 wire, two meshes to the inch. The large apparatus should be made of seven-eighths inch stock, and the accompanying wire netting should be made of No. 12 wire, one mesh to the inch.



TRE 3.—General plan for three sizes of reactive tendency apparatus. S, small apparatus; M, medium apparatus; L, large apparatus. X, center of circles on arcs of which reaction boxes and outer alley walls are apparatus; D, E, F, alleys for small apparatus; B, release box for medium apparatus; C, release box for large doors for the three sizes of apparatus are shown); 14, door between release box C and alley F.

All stock should be planed on both sides, and the apparatus should be given two or three coats of dark gray paint, if it is to be exposed to the weather. If, instead, it is to be used indoors, it should be painted white or gray, according to the degree of illumination of the experiment room.

The walls of the reaction chamber should be made of wire netting of the weight indicated above. The outer walls of the alleys may be made of wood or wire netting. The release box should be built of wood except for the wire netting cover and door. The entrance and exit doors should be made of wood.

In table 1 are presented the chief dimensions for the three sizes of apparatus under consideration.

Table 1.

Principal Dimensions in Centimeters or Inches of Convertible Reactive Tendency Apparatus

			-	-			
Measurements Of reaction boxes		sions or nall	Dimer for Med		Dimensions for Large		
Width outside	10	cm.	30	cm.	60	cm.	
Width inside (minimum)	7.5	cm.	- 25	-em.	51	cm.	
Length outside	30	cm.	60	cm.	140	cm.	
Length inside	29-	cm.	58-	cm.	135-	cm.	
Depth outside	20	cm.	40 .	cm.	200	cm.	
Depth inside	19+	cm.	38+	cm.	198-	cm.	
Of entrance and exit doors							
Width	8.4	cm.	27	cm.	54	cm.	
Length	20	cm.	40	cm.	200	cm.	
•							
Of release box					400 .		
Width	33 +	cm.	99十	cm.	198 +	cm.	
Length	30	cm.	60	cm.	140	cm.	
Depth	20	cm.	40	cm.	200	cm.	
Of release box doors					_		
Width	10	cm.	30	cm.	60	cm.	
	20		40		200		
Length		cm.		cm.	200	cm.	
3 For details see Rehavior Mono	graths.	vol. 3. 1	no. 1. p.	14.			

Measurements Of alleys Width inside Depth	Dimen for Sma 10 20		Dimens for Mediu 30 40	,	Dimer fo Lar 60 200	or
Distance from center X to entrance doors Distance from release doo	r				687.1	
to entrance doors Of strips for doors to slide Thickness Width Length		in. cm. cm.	1/2		635.1 7/8 6.5 200	in.
Block for reward mechanis Width Length Depth	6 10 2	· cm. cm.	10 30 4	cm.	15 60 6	cm. cm.
Hole in block Diameter Food cup Diameter at top Depth Cover for food cup	4 + 2	cm.	6+ 6 4	cm. cm.	7+ 7 6	cm.
Width Length Space necessary for appara	atus in		14 (4	cm. +10)	25 (1	cm. 0+15)
WidthLength	10 12	ft.	20 20	ft. ft.	30 ft 36	ft.

Certain suggestions concerning details of construction are of practical importance. It is desirable, for the sake of uniformity, to supply each box with a floor. This floor should be cut shorter than the sides of the box so that the entrance and exit doors may drop past it, thus discouraging attempts of subjects to raise the doors. Or, if the floor is cut full length, a strip nailed across the box just inside of the exit door will serve the same purpose while giving support to the floor.

Each box should have a wire netting cover on top.

All doors should slide vertically, upward, in wooden ways. These are conveniently made by nailing strips of wood to the side walls of the box. The strips serve the additional purpose of supporting the side walls. The outside strip may either be nailed to the end of the side wall or along the side. If nailed to the end, it serves as the outside strip for adjacent doors and thus reduces the amount of labor. In figure 2, the outside strip for the entrance door is shown as nailed to the end of the side wall. The writer prefers this method of construction.

The reward receptacle, or mechanism, must be so constructed as to be concealed when the exit doors are down and fully exposed when they are raised. It may be simply and conveniently constructed by nailing outside the rear end of each box a block of wood, of the dimensions suggested in the table, in the center of which there is a hole large enough to receive a metal food cup. Aluminum is preferable as material for the food cup, and desirable dimensions for the various sizes of apparatus are suggested in table 1. In the proper position on the outside of the exit door, there should be screwed a metal plate, bent at right angles in such wise as to cover completely and tightly the food cup when the exit door is down. This is shown in figure 4.

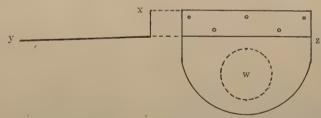


FIGURE 4.—Metal cover for food cup. w, position of food cup under cover; z, point at which cover is bent nearly at right angles; x, portion of cover which is attached to exit door by means of wood screws, holes for which are indicated; y, portion of cover which hides food cup.

The dimensions for this cover or cap for the food cup, also, are indicated in table 1. For the small apparatus, heavy tin is a satisfactory material for this cover; for the medium apparatus, light galvanized iron suffices; and for the large apparatus, it is necessary to use galvanized iron which is so thick that the large apes cannot readily bend the cover out of shape. The thickness should be about 1/16 inch.

For most animals there is no necessity of locking the doors of the apparatus, but when it is to be used with monkeys or anthropoid apes, it is absolutely necessary that the experimenter be able to securely lock any one or all of the sliding doors. It is therefore essential to equip the large sized apparatus with locks to be operated in connection with the mechanisms which raise and lower the doors. Each door should lock automatically when lowered and unlock when the raising mechanism is operated.

Just behind and a trifle above the release box, an observer's stand or record table should be constructed, separated by a screen from the apparatus so that the animal shall not be able to see the observer. On this table there should be placed a keyboard, or lever device, by means of which any one of the twenty-six working doors of the apparatus may be raised or lowered quickly and quietly.

For the small apparatus the various doors may be controlled readily by means of a light cord, which runs from a screw eve in the top of each door, through appropriately placed pulleys, to a hinged lever key which the observer operates. This key should be so arranged that when it stands in approximately vertical position the entrance door is closed. When it is placed in the horizontal position, the entrance door is open. A cord from the exit door, carried similarly by pulleys, should be so placed that it may be attached readily by means of hook and ring, or ball and slot, to this key, so that if, when a given entrance door is lowered, the experimenter desires to raise, simultaneously, the exit door of the same box, the pushing of the key to the vertical position will effect the appropriate movement of each door, that is, will simultaneously lower the given entrance door and raise the given exit door. The distance to which the entrance door is raised may be altered by changing the point of attachment of the cord to the key. This simple hinged key and cord device renders necessary the use of only fourteen keys for the operating of twenty-six doors, but the scheme is feasible only so long as the doors in question are light enough to be readily moved by means of a fairly small lever key. The accompanying diagram, figure 5, indicates the relations of parts, as described above.

⁴ If both return alleys are used there are twenty-seven doors instead of twenty-six to operate.

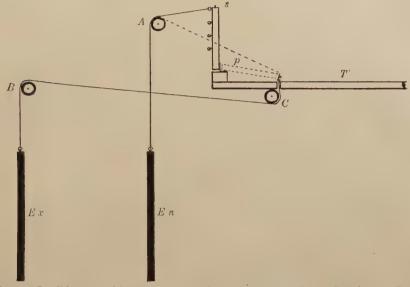


FIGURE 5.—Diagram of lever-key mechanism for raising and lowering doors. En, entrance door; Ex, exit door; T, observer's table; s, hinged lever key in vertical position; p, same, in horizontal position; A, pulley for cord between entrance door and lever key; B, pulley for cord between exit door and lever key; C, second pulley for cord from exit door.

For the medium sized apparatus also, the lever key mechanism is feasible, but it requires considerably more space and much greater effort on the part of the experimenter. A substitute for it is the weighted cord mechanism. A cord with appropriate carrying pulleys is provided for each door, and to the end of the cord, which drops in front of the experimenter's table and within easy reach, is attached an iron or lead weight which is just sufficient to hold the door in position after it has been raised by the experimenter. If the weight is too heavy, the door will tend to rise at inappropriate times; if too light, it will not stay in position after being raised. This device has the defect of varying in reliability with humidity and temperature, since the door will slide more or less easily in accordance with these varying conditions. The lever mechanism is preferable,

⁵ Described in previous papers on the multiple-choice method. A study of the behavior of the pig Sus Scroja by the multiple-choice method, Journal of Animal Behavior, 1915, 5, p. 188. The mental life of monkeys and apes: a study of ideational behavior, Behavior Monographs, 1916, 3, p. 14.

since it can be relied upon to place and hold the doors in a

constant position.

For the large apparatus, it is extremely desirable to devise some type of lever mechanism which shall be easily manipulated, reliable, and inexpensive. All of the mechanisms thus far proposed are either too cumbersome or too expensive to be feasible, but it is hoped that shortly a method may be discovered by which the experimenter may conveniently and accurately control the various doors by means of levers, the maximum excursion of which shall not exceed eighteen inches. Since the various doors must be raised a maximum of seventy-two inches, it will probably be necessary to introduce one or more forms of multiplying device. Already an automatic locking device, to be operated in connection with the proposed system of levers, has been designed.

In the absence of a satisfactory scheme for the use of levers, weighted cords and locks, which are operated independently, may be employed. But this system of control mechanism, as has been stated above, is both unreliable and troublesome to operate because of the numerousness of the parts. There must be a separate weighted cord for each of the twenty-six doors and a separate lock mechanism for each of the twelve boxes, entrance and exit door in each case being controlled by the same lock.

USE OF APPARATUS

The use of the convertible reactive tendency apparatus in connection with each of the three methods in question will now be described. For all of the methods alike, rewards and punishments may be used as inducements to effort. As rewards, food presented in the food cups, or for children small presents similarly presented, serve well. In certain exceptional instances, it may prove desirable to present the reward for a successful choice, not in the food cup of the correct box, but instead at the entrance to the release box. As punishment, it has proved feasible to use confinement in incorrect boxes. It seems probable that for certain organisms the electric shock may prove useful.

Hamilton Method

For use with the Hamilton method of quadruple choices, the following procedure is suggested. This method involves the use of only four reaction mechanisms. Boxes 5, 6, 7 and 8 may

therefore be used, the fact that they are to be reacted to being indicated by their openness, the entrance doors being raised in case of each trial. Since the entrance doors of all other boxes should remain closed and locked, there would be no persistent tendency on the part of most organisms to attempt to enter other than the four boxes referred to. For some purposes, it may prove even more satisfactory to use boxes 2, 5, 8 and 11.

Incorrect choices would not be rewarded, and as seemed desirable the subject could be punished for such choices by being confined in the boxes for a stated period. A correct choice, no matter what the particular form of the problem, would naturally be rewarded by the presentation of food in the food cup.

Various problems, in addition to that originally suggested by Hamilton, may be presented by this method. The following will suggest the range of possibilities: (1) An insoluble problem, such as Hamilton used, the several boxes serving as correct boxes in irregular order, but the same one never twice in succession and each the same number of times in every hundred trials (this problem is practically insoluble by even the most intelligent organism): (2) the systematic use, as correct box. of each in turn from the left end to the right end, that is, 5, 6, 7, 8, or in case of the other group of boxes, 2, 5, 8, 11, this succession being repeated indefinitely; (3) box at left end, box at right end, box next to left end, box next to right end, the same being repeated indefinitely. From these suggestions, it is evident that various degrees of complexity of order and relationship might be utilized to elicit reactive tendencies and to display problem solving ability of different sorts.

The apparatus demands no special modification or adaptation for use in connection with the Hamilton method. Further details are unnecessary in view of the fact that Hamilton has already published a fairly complete description of method and apparatus,6 and has in press a still more elaborate account of procedure and results.7

Hunter Method

For the method of delayed reaction the apparatus demands certain special appliances which, however, do not have to be removed when either the Hamilton or the Yerkes method is

⁶ Hamilton, G. V. A study of trial and error reactions in mammals. *Journal Animal Behavior*, 1911, 1, pp. 33-66.

⁷ Behavior Monographs, 1917, 3, no. 13.

in use. The special equipment consists of a concealed incandescent electric lamp for the illumination of each box and an electric signal and timing mechanism for the operation of the lamps and the door between the release box and the reaction chamber.

The method of delayed reaction may be used with various groups of doors, according to the grade of difficultness of response desired. Thus, as the simplest situation, boxes 6 and 8 may be used. In this case, the entrance doors of both boxes should be raised in preparation for a trial. The doors of the other boxes should remain closed. In accordance with a prearranged plan, either the one or the other box would be indicated, by momentary illumination, as the box to be chosen.

For the second grade of difficultness, boxes 5, 6, 7 and 8 might be used, each of them having the necessary equipment and connections for use as the correct box; for grade three, boxes 2, 5, 8 and 11; for grade four, boxes 1, 3, 5, 7, 9 and 11; and for grade five, all of the twelve boxes might be subject to use, that is, the entrance door of every box should be open and the subject should be required to choose that one of the twelve which has previously been illuminated.

The satisfactory use of this method necessitates not only the presence of a lamp, but the installation of a mechanism which shall control several important factors in the situation. The experimenter, by pressing a simple key, should close a circuit which at once illuminates a certain box (the particular box to be determined by the setting of a switch), and at the same time starts a timing mechanism. This mechanism should, after an interval, with a range of 1 to 10 seconds, open the lighting circuit, thus cutting off the illumination of the correct box; and after an interval of 0 to 60 seconds it should cause the door of the release box to open so that the animal may enter the reaction chamber. For intervals longer than 60 seconds, it seems best to have the experimenter determine the delay by means of a stop watch and operate the door of the release box by hand.

There is no obvious reason why this twelve mechanism reactive tendency apparatus should not be used in wholly satisfactory fashion for the study of delayed reactions. The additional electrical equipment should in no wise interfere with the other uses of the apparatus and that portion of it which controls the release box door might be made to serve the experimenter in connection with all of the methods.

Yerkes Method

For use by the method of multiple choices, the apparatus demands neither modification nor special adaptation. The chief features of the method have already been described several times, and it is needless here to do more than formulate a set of problems with wider range of difficultness than those heretofore used in reported experiments on lower animals. Those proposed problems, ten in number, are presented in brief form below, with a series of ten settings for each. Thus, in case of problem 1, for which the correct mechanism is always box number 5, that is the fifth from the left end of the apparatus, the first setting involves the use of boxes 1 to 6, the second setting, of boxes 3 to 12, and so on. It is understood that, if possible, this series of ten settings (ten trials) shall be presented to a subject once a day until the problem has been solved. If for any reason the series of ten trials cannot be completed on a given day, it should be resumed from the point of interruption on the following day. If more than one series per day can be given, either the ten trials may be divided into two groups of five each or the total series may be repeated.

In each of the series of ten settings, a total of sixty boxes—is presented. The average number of boxes open in each trial is, therefore, six. Of these—sixty boxes, ten are definable as correct boxes. The probability of correct first choice prior to experience is for any series of ten trials, one to five. In order that this ratio of probable right to wrong first choices shall not be disturbed, it is desirable that the experimenter make use of the proposed settings.

Proposed Problems and Settings for Multiple-Choice Method

```
Problem 1. Same box (box 5).

1-6 (5); 3-12 (5); 4-6 (5); 5-9 (5); 2-10 (5);

4-5 (5); 4-10 (5); 3-6 (5); 1-8 (5); 5-10 (5).

Problem 2. First at left end.

6-12 (6); 11-12 (11); 3-11 (3); 1-5 (1); 4-11 (4);

10-12 (10); 5-9 (5); 2-12 (2); 8-11 (8); 7-12 (7).

Problem 3. Middle.

1-7 (4); 10-12 (11); 6-10 (8); 1-11 (6); 1-3 (2);

4-10 (7); 1-9 (5); 9-11 (10); 1-5 (3); 6-12 (9).
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Problem 4. Third from right end.
1-6 (4); 5-8 (6); 3-12 (10); 1-3 (1); 7-11 (9);
2-10 (8); 1-7 (5); 3-5 (2); 2-9 (7;) 1-5 (3).
```

Problem 5. Alternately left end and right end. 8-12 (8); 1-10 (10); 3-8 (3); 6-9 (9); 1-9 (1); 3-5 (5); 7-11 (7); 5-12 (12); 2-8 (2); 4-6 (6).

Problem 6. Progressively from right to left end of apparatus—toward left by ones.

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10-12 (12); 6-12 (11); 3-10 (10); 8-12 (9); 8-10 (8); 1-9 (7); 5-8 (6); 4-9 (5); 2-11 (4); 3-7 (3).
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Problem 7. One place to left of middle key. 6-12 (8); 3-5 (3); 8-12 (9); 1-9 (4); 2-12 (6); 10-12 (10); 5-11 (7); 1-5 (2); 3-9 (5); 1-3 (1).

Problem 8. Alternately second from right and second from left. 6-12 (11); 2-5 (3); 1-8 (7); 5-9 (6); 1-5 (4); 4-12 (5); 5-10 (9); 9-11 (10); 2-9 (8); 1-5 (2).

Problem 9. To the right of mid-point in even group; or first member of second-half of group.

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3-10 (7); 1-4 (3); 2-7 (5) 1-2 (2); 3-12 (11); 8-11 (10); 5-12 (9); 1-10 (6); 5-10 (8) 11-12 (12).
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Problem 10. Alternately to left of middle key and to right of it. 1-7 (3); 8-12 (11); 2-10 (5); 10-12 (12); 1-9 (4); 3-9 (7); 1-3 (1); 6-10 (9); 6-12 (8); 3-7 (6).

The various forms of problem serviceable in connection with the different methods and the detailed procedure for each remain to be worked out. The methods have been thoroughly tried out and have already yielded such valuable results that further development and application is obviously desirable. There is no reason why the same apparatus should not henceforth serve for studies of reactive tendencies and ideational behavior by the method of quadruple choices, that of delayed reaction, that of multiple choices, and that of conditioned reflexes.

We experimenters shall doubtless do well to use our devices to the limit of their applicability, seeking no less assiduously new ways of employing existing experimental equipment than we seek to invent new mechanisms.

LIGHT REACTIONS OF THE CRIMSON-SPOTTED NEWT, DIEMYCTYLUS VIRIDESCENS

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INTRODUCTION

The following experiments, which are extensive rather than intensive in character, were started with a dozen salamanders obtained in the month of November from the Marine Biological Laboratory at Woods Hole. During the course of the experiments, which extended over a period of more than a year, three of the animals escaped, so that some of the later results were obtained with only nine animals; they were obtained from Woods Hole because of their comparative rarity in the neighborhood of Morgantown when the work was begun. Later, animals were caught in a local pond and these were also used in the experiments.

No change in reaction, except in one possible case, was produced by prolonged residence (for a month or more) in a photographic dark room, though it was noted that all of the animals were of a lighter shade of color when first brought from the dark room.

In all but one or two cases the animals were confined in a rectangular glass aquarium, six inches wide by ten inches long, with two or three inches of water. The water was used chiefly for two reasons: because the newts were very much more active in the water than they were in the empty aquarium, and because the water, of course, acted as a heat-screen and practically eliminated heat as a stimulus.

A few tests were made without water, with no noticeable difference in reaction except speed; the animals responded two or three times as quickly when in water than they did when in the merely moistened aquarium.

Observations made upon animals in an evenly illuminated aquarium seemed to show that they have a certain tendency

to collect in groups, in one place or another, without regard to the light stimuli to which they are subjected; this tendency, then, has no apparent bearing upon the following experiments.

After hundreds of observations, extending over a period of many months, upon several lots of animals, several sets of observations were made upon one or two small groups of animals immediately upon bringing them into the laboratory from their native pond. Under these conditions the animals responded either very indefinitely to the same light stimuli, or even in a contrary manner to the animals that had been for some time under observation. This irregularity in what had been considered the normal response was also noticed in a group of animals that had been in the aquarium for a long time and had not been used in the experiment for a considerable period.

It is possible that, after all, the responses of the animals under these abnormal conditions may be quite different from what would be seen under normal conditions in their native habitat.

It is the intention of the author to carry on similar experiments upon this species in the natural environment as soon as a suitable spot can be found. (See Addendum.)

Experiment I.—This experiment was to determine whether Diemyctylus is positively or negatively phototropic towards white light.

Twelve animals were placed in the above-described aquarium of water which was entirely surrounded by black except over half of the top. Ten inches above the surface a 25-watt, 115-volt tungsten lamp was so fixed as to illuminate exactly one-half of the aquarium, the other half, of course, being thrown in dense shadow.

At regular intervals of five minutes the numbers of animals in both light and dark ends were noted. When an animal, at the moment of observation, happened to be partly in light and partly in shadow it was counted for that region in which the greater part of its length lay, though occasionally an animal was so near the exact center that it was not counted on either side.

Table I shows that in 30 observations 95 animals were found in the light and 250 in the dark. These observations were

taken on three different days; and after observations 5, 7 and 17 the light and dark ends were suddenly interchanged, thereby throwing the larger proportion of the animals, that had collected in the shadow, into the light. The last five observations were made about two weeks after the first, during which time three of the animals had escaped.

						TA	BLE	ΞI									
Observation Light half Dark half	2	3	4	2	2	2	0	0	1	2	()	4	2	2	5	2
Observation Light half Dark half	1	2	6	4	5	4	3	5	4	1	4	8	9	5		ī	tals 95 250

Another set of observations made under the same conditions, except that only enough water to moisten the bottom of the aquarium was used, gave 141 animals in the light to 243 in the dark region. As noted above, without enough water to swim in the newts are so sluggish that experimentation is not nearly so satisfactory as when they are actively swimming.

It is evident, then, that, at least under the conditions of the experiment, these newts are negatively phototropic.

Experiment II.—Variations of experiment I were tried to determine the effect of temperature upon the phototropic reactions of Diemyctylus.

The first variation was merely to start the observations, made upon eleven animals, with the water at 10° C., the arrangement of aquarium and lights being as in experiment I. Not only was the aquarium surrounded by black, but the experiment was performed in a photographic dark room. Beween the 15th and 16th observations was an interval of two hours, during which time the animals were in the dark. After the 30th observation, when all the animals were in the dark half of the aquarium, the ends were reversed, throwing all the animals into the light half. When the animals, as in this case, were sluggish it would be some time before they would move into the dark again, which would reduce the total preponderance of dark over light. The total figures for 40 observations were 174 in the light end to 278 in the dark, which was about the proportion noted in experiment I when no water was used. At the end of

this part of this experiment the temperature of the water had risen about 2° C.

In the second variation of this experiment the aquarium containing the animals was placed out-of-doors for about five hours, until the temperature of the water had fallen to 1° C; it was then brought into the dark room where the same arrangement for vertical illumination of just half of the aquarium as in experiment I was used. All of the animals at this temperature were numb with cold, and lay motionless on the bottom of the aquarium. One or two were apparently dead and when turned over, ventral side up, made no effort to right themselves. At the beginning of this series of observations six animals were placed in the dark end of the aquarium and five in the light end.

TABLE II ¹														
Observations Light half Dark half	1 5 s	2 5 s 6	3 5 8 6	4 5 8 6	5 5 8 6	6 4 S 7	7 4 S 7	8 4 s 7	9 4 s	10 4 s 7	11 4 s 7	12 4 s 7	13 4 s 7	14 4 s 7
	S	S	S	S	S	S	S	S	S	S	S	S	S	S-
Observations Light half	15 6 S	16 6 s	17 6 8	18 7 S	19 2 S-			22 0	23 0	24 0	25 10 S-		27 4 A	28 4 A-
Dark half	5 S	5 S	5 S	4 S	9 S-	9 S-	10 S	11 A-	11 A-	11 A	1 s	4 S-	7 S	7 S
Observations Light half	29 3 A	30 0	31 0	32 5 S-	33 5 a	34 4 A-	35 2 - A-	36 2 S	37 5 a	38 2 A	39 3 a	40 1 A	41 1 A	42 1 A
Dark half	8 S	11 S	11 S	6 S-	6 S-	7 S	9 A-	9 S	6 a	9 A	8 A-	10 A-	10 A-	10 A
Observations Light half	43 0	44 6 A	45 4 A-	46 4 A	47 5 A	48 3 S	49 3 S-	50 1 A-	51 5 a	52 7 a	53 6 a	54 6 a	55 8 a	56 . 8 a
Dark half	11	5 S	7 A-	7 s	6 S	8 A-	8 S-	10 A-	6 A	4 A	5 a	5 A	3 a	3. A
Observations Light half	57 5 a	58 6 A	59 2 A	60 9 A	61 5 A	62 9 a	63 5 a	64 ' 2 a	Total 259			,		
Dark half	6 A	5 A	9 A	2 A	6 A	2 a	6 a	9 A	446					

Observations were begun at intervals of three minutes, but ¹ In this and the following experiments the letters refer to the average activity

of the animals at the time of observation—

a — very active; A — less active; A — still less active.

s — very quiet; S — less quiet; S — still less quiet.

A— and S— would probably be about the same state of activity.

as no change of position had taken place at the end of fifteen minutes the interval between observations was changed to five minutes, from observations 7 to 21, after which it was again made three minutes.

It will be seen from table II that, for the first 18 observations, lasting about one and one-fourth hours, there was very little change in the position of the animals, which lay almost motionless during that time. At the 18th observation the temperature of the water had risen to only 7° C., and warm water was carefully added until that in the aquarium was raised to 13.5° C.; the animals soon began to become more active, and after twenty minutes (22nd observation) all were collected in the dark half of the aquarium. From the 22nd observation until the end of the experiment observations were made at intervals of three minutes. It will be seen by table II that the light was changed after the 24th observation, throwing all the animals into the light end; after fifteen minutes all the animals had again collected in the dark region.

After the 31st observation, when the water of the aquarium had risen to 15° C., warm water was again added until that in the aquarium was raised to 24° C.; this operation was repeated after the 36th observation and the temperature raised to 33° C. The animals were mostly very_active but continued to collect in the dark region, so that after the 43rd observation, when all were in the dark, the ends were reversed, throwing all the animals in the light end.

After the 50th observation, when ten of the eleven animals were in the dark region, enough water was added to raise the temperature to 36.5° C.; this caused the animals to become unusually active, to frequently give a squeaking sound, and to come to the surface for air. After this, it will be noticed from the table, there is no longer a tendency to collect in the dark, possibly a slight tendency in the reverse direction. After the 59th observation water was again added until that in the aquarium was raised to to 38° C. At this temperature the animals acted as just described, but with more vigor. Some of them were so seriously affected that they turned ventral side up and could scarcely right themselves again, and it was evidently impossible to further increase the temperature without endangering the lives of the animals.

It is apparent, therefore, that low temperatures, not far above the freezing point of water, cause these animals to become so sluggish as to be more or less indifferent to differences of light and darkness. As the temperature rises they become active and seek the dark region of the aquarium. When the temperature reaches about 36° C. they become abnormally active and again become indifferent to light and shade differences. At somewhat less than 40° C., about the temperature of human blood, (though they could doubtless be acclimated to higher temperatures) they are seriously affected or possibly killed.

Experiment III.—Another variation of experiment I was to determine whether the animals would seek the dark half of the aquarium when the illumination was from below.

The same aquarium and eleven animals were used as in the preceding experiments, but the light was thrown from below by the same tungsten lamp, placed six inches below the bottom of the aquarium. In all, 60 observations, at three-minute intervals, were made, with a rest of three and one-half hours between the 30th and 31st observations. The temperature of the water was about 27.5° C. and the animals were active throughout the experiment, those in the light being the more active, on the average. The total number of animals counted in the light was 266; those in the dark, 360.

It is evident then, that Diemyctylus tends to come to rest in the dark region of the aquarium when the light comes from below, but that the tendency is not so strong as when the source of light is above the water.

Experiment IV.—This experiment was to determine the reaction of Diemyctylus in relation to the direction of white light.

In this and similar experiments both the region of the aquarium where found and the position of the animal in relation to the direction of the light were noted. It was noticed that when the aquarium, described on page 29, was placed with one end about eight feet from a window, but not in the direct sunlight, on a fairly bright day, a large proportion of the animals stayed in the end of the aquarium towards the light and swam against the glass as though trying to get nearer the window. No actual counts were made in this observation.

	TABLE III												
Observations		1 8 A-	2 8 A-	3 6 A-	4 7 S-	5 7 A	6 6 A	7 7 A-	8 7 A	9 7 A-	10 6 A-		
Facing dark		3 S	3 S	5 S	4 S		5 A-	4	4 S-	4	2 S		
In light end		7 A	6 A-	4 - A-	5 A-	7 A	5 A-	6 A-	8 A-	$\stackrel{4}{A}$	4		
In dark end		4 S	5 S-	$\bar{7}$	6 S	4 S	6 A-	5	3 S-	7 S-	7 S		
Observations	11 5 a	12 4 A	13 6 A	14 9 A-		.6 6 a	17 8 A	6	.9 9 A–		otal 136		
Facing dark	4 S-	4 S	1 S	2 S		4 S-	3 S-		2 S-	5 S-	68		
In light end	5 a	4 A	6 A	7 A-		7 A	8 A	6 A	7 a	6 : a	119		
In dark end	6 S-	7 S	5 S	4 S	4 S	4 S-	3 S	5 S	4 S	5 S-	101		

Table III shows the results of a series of observations upon the same eleven animals used in the preceding experiments. The aquarium, containing a few inches of water, was entirely surrounded by black except at the end which was towards the window, in this case twenty feet away. The day, while not dark, was overcast, and the light that entered the open end of the aquarium was naturally quite dim. When an animal, at the instant of observation, lay at right angles to the direction of the light it was not counted. It will be seen that exactly twice as many animals faced towards the light as faced away from it, while the number of animals in the half of the agaurium near the window was not very much greater than the number in the other half. It will be noticed also that, as a rule, the animals facing the light were more active than those facing in the other direction, and that those in the half nearer the light were more active than the others.

This experiment shows that these salamanders are positively phototactic even towards weak daylight.,

Experiment V.—This experiment or series of experiments was to determine the reaction of the animals towards a much more intense white light than the daylight of the preceding experiment. The light here used was the same 25-watt, 115-volt tungsten lamp that was used in experiment I; it was placed six inches from the open end of the aquarium. The aquarium

was surrounded except at one end by a black cloth, and the whole apparatus was operated in a photographic dark room. Observations were made at intervals of five minutes. The temperature varied from 16.5° C. to 19° C. Eleven animals were used. At the beginning of the experiment the animals were quiet and equally distributed through the aquarium.

		T	ABLE I	V				
Observations Facing light	1 2 7 10 S- A-	3 9 - A-	4 5 7 10 a A	6 10 A	7 8 8 10 a A	9 10 9 7 A A	7 8	12 13 8 4 A A-
Facing dark	1 1 S S	2	4 1 S- A-	1 S	3 1 S- S	2 S- S	3 S- S-	3 7
In light end	7 8 S- A-	7 - A	7 8 a A		10 8 A a	7 (a a		5 4 a A-
In dark end	4 3 S S-	4 A-	4 3 S- A-	3 S-	1 3 S S	4 S- 5	2 - S	6 7 S A-
Observations Facing light	14 15 6 9 A- A	16 10 A	17 18 7 10 A A	8	20 21 8 9 A a	22 23 10 3 A A	3 11	25 26 9 9 A- A-
Facing dark	3 2 A- A-		2 1 S- S	3 S	2 2 S S	1 3	0	2 2 S S
In light end	5 7 A- A	6 A	7 6 a A	8 A	8 9 A a	6 4 a a		9 8 A a
In dark end	6 4 A- A	5 A-	4 5 A- S-	3 S	3 2 A S-	5 S- S	7 4 S- S-	2 3
Observations Facing light			9 30 8 7 A A-	31 32 8 9 S 5		34 35 7 5 A- A	36 5 A	37 Totals 4 298 A-
Facing dark	. 1 S	3 S	2 4 S S	3 S		4 6 S S	6 - A-	2 90 A-
In light end			9 7 A A-	4 A	_	4 5 A A-	3	4 244 A
In dark end	. 2 S		2 4 S S	7 7 5 S	7 7	7 6 S S-	8	7 163 A
For explanation of lett	ers see	page 3	2.		*	,		

Observations 1 to 12 were made at night; the other observations during the morning and afternoon of the following day. Between observations 22 and 23 was an interval of two hours and five minutes during which the tungsten light was shining into the end of the aquarium. After observations 9 and 25 all the animals were gently pushed into the end of the aquarium away from the light. After observation 12 and about one hour before observation 13 the animals were fed as much raw meat as they would eat. It will be seen from table IV that the average activity of the animals facing the light was greater than

that of the animals facing away from the light; and that the animals in the near half of the aquarium were, as a rule, more active than those in the half farther from the light. As before, animals which lay, at the moment of observation, with the long axis at right angles to the direction of the rays of light were not counted. The total number of animals facing the light was 298, to 90 that faced away from the light; the number in the near half of the aquarium was 244, to 163 in the half farther from the light.

Experiment VI.—Another series of 25 observations, taken every five minutes, under conditions similar to those just described, except that the aquarium was in an ordinary room and covered with the same black cloth, gave 200 facing the light to 78 facing away from the light, and 179 in the near end to 97 in the far end of the aquarium.

Experiment VII.—Still another series of 30 observations, taken every five minutes, was made upon nine of the same animals after having been in the dark for 32 days except for about two and one-half hours three days before the present experiment. This was to determine if prolonged residence in total darkness had any effect upon their reaction to white light. The arrangement of the apparatus was the same as in experiment V. One hundred and ninety-seven animals were found facing the light, to 72 facing away from the light; 202 were in the near half, to 74 in the far half of the aquarium.

It will be seen by comparison with experiment V that, after this long residence in darkness, the preponderance of animals that faced the light over those that faced in the opposite direction was less than in animals that had been in the light; while the preponderance of animals in the near half of the aquarium over those found in the distant half was greater in animals that had been in the dark than in those that had been in the light. It is possible that these differences may have been due to other causes than the prolonged residence in the dark.

Experiment VIII.—To see whether the same eleven animals were positively phototactic to a light of even greater intensity than the tungsten the aquarium, covered as before, with a black

cloth, was placed, in a dark room, with its open end fifteen inches from the lens of an arc projection lantern. Observations were taken at five-minute intervals. At this distance the light was, of course, decidedly painful to the human eye.

The positive response was so marked that only 15 observations were made, which gave 116 facing towards the light to 41 facing away; and 105 animals in the near half of the aquarium to 60 in the distant half. The animals facing the light and in the near half were, as a rule, somewhat, though not a great deal, more active than the others.

It appears, therefore, that the response to white light is about the same whether the source of light be dim daylight or an intense electric arc.

Experiment IX.—This experiment was to determine the effect of low temperature upon the responses of Diemyctylus to white light at the end of the aquarium.

				4	TAE	LE	V			•				
Observations Facing light	1	2	3	4 1 S	5 0	6	7 7 S-	8 2 - S -	9 2 A-	10 3 A-	11 5 S-	12 2 S-	13 3 S-	14 0
Facing dark				10 S-	11	11	4 S-	. 9 . S-	9 A-	8 S-	6 S-	9 S-	8 S-	8 - A-
In near end	· ·	·s	·ś	1 S	0	0	7 S-	6 S-	5 A-	6 S-	7 S-	4 S-	3 S -	0
In far end	s	Ġ	ŝ	10 S-	- 11 - S-	- ¹¹ / _S	4 S-	5 S	6 A-	5 S-	4 S-	7 S-	8 S-	11 A-
Observations Facing light	15 0	16 2	17 4	18 4	19 6 S	20 2 A-	21 - A-	22 3 - A-	23 4 A-	24 3 A-	25 3 A-	26 2 A-	27 5 A-	28 4 - A-
Facing dark	4 A-	4	3	3	4 S	7 A-	7 - A-	7 · A-	4 A-	7 A-	8 A-	7 A-	4 A-	
In near end	0	0	0	0	10 S	7 A-	7 - A-	4 - A-	4 A-	2 A-	2 A-	2 A-	2 A-	2 A-
In far end	11 A-		11	11 S	s S	4 A-	- A-	7 - A~	7 A-	9 A-	9 A-	9 - A-	9 A-	9 - A-
Observations Facing light		29 4 A-	30 4 A-	31 3	32 5 A-	33 7	34 2	35 4 A–	36 4 A-	37 6 A-	38 3 A-	39 3 A-	40 T 6 A	otals 122
Facing dark	• •	5 A–	5 A-	6	6 A-	4	9	7 A–	6 A-	5 A-	8 A-	5 A-	3 A	231
In near end		3 A-	3 A-	8	5 A-	6	7	5 A-	5 A-	5 A-	5 A	4 A-	3 A	140
In far end		8 A-	8 A-	2	6 A	5	4	6 A-	6 A-	6 A-	6 A-	7 A-	8 A	266

The same animals and arrangement of apparatus were used as in experiment V, the only difference in the experiments being that in the present one, table V, the aquarium containing the animals had been placed outdoors for three hours, until the temperature of the water had fallen to 0° C. and a thin skim of ice had formed.

As in experiment II the animals at the beginning of the observations were all stationary, as though dead, and were evenly scattered over the bottom of the aquarium. Observations 1 to 6 were taken at ten-minute intervals; 7 to 40 were at five-minute intervals. After observations 5, 17 and 30 the ends were reversed, thus putting the animals from the far to the near end of the aquarium; this, of course, raised the total number for the far end and lowered the total number for the near end. For the first 3 observations, or one-half hour, practically no change in the position of the animals took place; at this point warm water was carefully added until the temperature of that in the aquarium was raised to 8.5° C., and by the end of the experiment the temperature had slowly raised until it was 12.5° C. After the addition of the warm water the animals began to show signs of life, though they remained rather sluggish to the end of the experiment.

In 40 observations 122 animals faced towards the light to 231 away from the light; 140 were in the near half of the aquarium, 266 in the half farther from the light.

Experiment X.—This was a continuation of the preceding experiment under exactly the same conditions except that the temperature of the water at the first observation was 4.5. C. instead of 0° C., and the animals were moving about very slowly instead of lying perfectly still. After the 4th, 5th and 14th observations all the animals were pushed into the near half of the aquarium. Observations were somewhat irregular, being every ten minutes for about the first half of the observation, every five minutes for the latter half of the observations. After observation 16 warm water was added until the aquarium temperature was 23.5° C.; the dark room being cold, this temperature was lowered 2° by the end of the experiment. In 28 observations 134 animals were found facing the light to 147 that faced away from the light; while 107 animals were counted

in the near half of the aquarium to 212 in the far half. It is noticeable, however, that in the 16 observations before the warm water was added 67 animals faced the light to 83 that faced in the opposite direction, while in the 13 observations after the addition of the warm water 67 animals again faced the light but only 64 faced away from it. Again, in the first 16 observations 50 animals were counted in the near half of the aquarium to 126 in the far half, while in the last 13 observations 57 animals were in the near half to only 86 in the far half.

Experiment XI.—This was a continuation of experiment X on the following day. The water at starting was 5.5° C. and was raised, after observation 12 to 23° by the addition of warm water. The first 7 observations were at somewhat irregular intervals of ten minutes; the remaining observations were at five-minute intervals. In 30 observations 149 animals faced the light to 154 that faced in the opposite direction; while 143 were noted in the near end to 198 in the distant end. In the first 12 observations, however, when the maximum temperature of the water was 11°, only 43 animals faced the light to 73 that faced away from it; while in the last 18 observations, when the water had been raised to 23°, 106 animals faced the light to 62 that faced the other way. Again, in the first 12 observations 48 animals were in the near half to 94 in the far half, while in the last 18 observations the numbers were 95 to 104 respectively. In a total of 98 observations for the last three experiments, 405 animals faced the light to 532 that faced in the opposite direction; and 390 animals were counted in the near half of the aquarium to 676 that were found in the far half.

From the last three experiments it seems that low temperatures tend to inhibit or even reverse the positive phototaxis of Diemyctylus as seen in movements towards the light and orientation of the body so that the animal faces the light.

Experiment XII.—This experiment was to determine the responses of Diemyctylus to white lights of different intensities acting simultaneously at opposite ends of the aquarium.

Nine of the same animals used in the preceding experiments were employed here; they had been in darkness for 15 days. The same aquarium in the same dark room was used; it was

entirely covered with black cloth except at the ends where the light entered. Two 25-watt, 155-volt tungsten lights were used; they were not tested as to candle-power, but they were of the same supposed power and were of the same age. One light was six inches from one end of the aquarium, the other light was twenty-four inches from the other end. The first 50 observations were taken at five-minute intervals, except that one and one-half hours intervened between observations 31 and 32, during which time the animals were in the darkness.

In 50 observations 265 animals were seen facing the more distant (24 inches) light to 170 that faced the nearer and, therefore, more powerful light. Two hundred and sixty-nine animals were found in the half of the aquarium nearer the more distant light, 174 in the region towards the nearer light. The weaker of these two lights, then, seems to have the greater attraction for the animals.

Experiment XIII.—The arrangements were exactly as in experiment XII except that the lights were six inches and twelve inches from their respective ends of the aquarium. Two and one-half hours in darkness intervened between observations 19 and 20. In 40 observations 141 animals were found facing the nearer (6 inches) light to 185 that faced the more distant light; while 163 were found in the half of the aquarium towards the nearer light, to 190 in the other half. The weaker of the two lights seems again to be the more attractive to the animals, though in a less marked degree than in experiment XII.

Experiment XIV.—The same experimental conditions as in the preceding except that the lights were twelve inches and forty-eight inches from their respective ends. Between observations 15 and 16 was an interval of three days, and between observations 45 and 46 was an interval of one day; during both intervals the animals were in the dark. As in the preceding experiment, the observations were taken every five minutes.

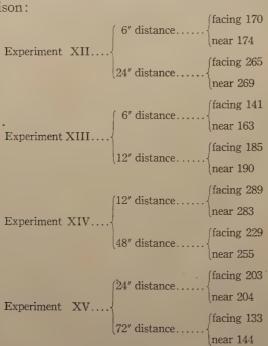
In 60 observations 289 animals were found facing the nearer (12 inches) light, to 229 that faced the farther (48 inches) light. Two hundred and eighty-three were seen in the half of the aquarium towards the nearer light, to 255 in the other half. It seems that, while the differences between these sets of figures

are not great, the nearer (12 inches) light has a somewhat greater attraction than the more distant (48 inches) light.

Experiment XV.—The conditions of this experiment were exactly the same as in the preceding except that the lights were twenty-four inches and seventy-two inches from their respective ends. There was an interval of twenty-one hours (in the dark) between observations 5 and 6. In 40 observations 203 animals faced the nearer (24 inches) light, to 133 that faced the farther (72 inches) light; and 204 were in the half of the aquarium towards the nearer light, to 144 in the other half.

Experiments XII to XV may thus be placed in tabular form

for comparison:



Experiments XII and XIII seem to indicate that when one of two sources of light is very intense the animals tend towards the less intense light; while experiments XIV and XV show that when neither source is very intense, perhaps not reaching a certain optimum, the animals tend towards the more intense light.

REACTIONS TO RED LIGHT

Experiment XVI.—In this experiment the same nine animals and the same arrangement of apparatus as in experiment V were employed; but between the tungsten lamp, placed six inches from the end of the aquarium, and the aquarium was a filter composed of two glass jars each 20 mm. thick containing an aqueous solution of crystal violet and of potassium monochromate respectively, after the formula of Landholt.

In 30 observations, taken at five-minute intervals, 225 animals were noted facing the red light to 46 facing away from the light; and 221 animals were found in the end of the aquarium nearer the light to 49 in the farther end.

Experiment XVII.—This experiment was an exact repetition of experiment XVI, made thirty days later, during which period the animals had been in the darkness of the photographic dark room. In 12 observations, at five-minute intervals, 86 animals faced the red light to 19 that faced in the opposite direction; and 82 were seen in the red end of the aquarium to 26 in the other end. Comparison of experiments XVI and XVII with experiment V shows that the proportion of animals attracted by the light was greater with the red light than with the white. This may have been due to the decrease in intensity rather than to the red color.

REACTIONS TO BLUE LIGHT

Experiment XVIII.—This experiment was performed thirty-six hours after experiment XVII; during the interval the animals were in complete darkness. The experiment differed from the other only in the substitution of a blue filter for the red. This filter consisted of two similar glass jars containing solutions of crystal violet and copper sulphate after Landholt's formulae. The five-minute intervals between observations were somewhat lengthened on four occasions by interruptions to the experiment.

In 30 observations 197 animals were found facing the blue light to 73 that faced away from it; 195 animals were found in the half of the aquarium near the light to 84 in the other half. It is evident that the proportion of animals attracted by the blue light is less than was attracted by the red light.

REACTIONS TO GREEN LIGHT

Experiment XIX.—The arrangement of this experiment differed from the last only in the substitution of a green filter for the blue. This filter consisted of solutions of copper chloride and potassium monochromate, after the formulae of Landholt, in jars like those described in the two preceding experiments. The same nine animals were used; they had been in total darkness for twenty-nine days, and had been fed upon earthworms the day before the experiment. In 30 observations, at five-minute intervals, 210 animals faced the green light to 51 that faced away from it; and 199 animals were found in the near half of the aquarium to 71 in the half farther from the light.

The attraction of the green light is apparently more marked than the blue but less marked than the red.

REACTIONS TO WHITE LIGHT ON VARIOUS PARTS OF THE BODY

Experiment XX.—In order to be able to throw a small, sharplydefined spot of white light on any part of an animal a small electric bulb was mounted in the tube of a microscope, as described by Bradley M. Patten in Science, January 22, 1915, pp. 141-2. By using different low-power objectives a sharply defined spot from 1 to 5 mm. in diameter was directed upon all parts of the body of several animals. These animals were in a black rubber developing tray in sufficient water to cover them. In one case they had been in a dark room only an hour; in another series of trials they had been in the dark for a week or more. Some of the animals were of the lighter shade with very bright crimson spots; other animals were of the darker type when experimented upon. During experimentation just enough light was admitted to the dark room to faintly see the animals, so that any movement could be noted. The spot of light was thrown, as has been said, on all parts of the body, from the head to the tip of the tail; on the crimson spots and between them: it was varied in diameter from 1 to 5 mm. No certain reactions could be determined for any of the animals used. Doubtful reactions were sometimes obtained when the spot was made large enough to cover the entire anterior half of the head.

When the spot was thrown on the black bottom of the tray near the animals they followed it actively and snapped at it, evidently taking it for food; they seemed to be able to see the spot at a maximum distance of about 3 cm.

Experiment XXI.—The same animals that failed to respond to the white spot from the microprojection apparatus responded promptly when a beam of sunlight was thrown, by a small mirror, upon various parts of the body. When the light was thrown upon the tail they either started forwards suddenly or drew the tail sharply forward along the side of the body. When the light was thrown upon the head the animal usually backed away from it. Animals in a cloth covered aquarium in a brightly lighted room responded about as promptly as those in the dark room.

Animals that had been for some time in the dark responded more promptly than those that had been exposed to the light; some of the former fairly jumped when the beam fell upon them.

Little or no response was obtained when a small beam from a 5 mm. mirror was used instead of a beam that was large enough to illuminate a large area of the animal at one time.

The animals responded in the same way, and almost as promptly, to a beam of light from below.

These reactions to a beam of sunlight are quite similar to those described by the author for Necturus (2).

SUMMARY

- 1. Under the conditions of these experiments Diemyctylus is almost always markedly negative in its phototropic reactions to white light, at ordinary temperatures.
- 2. At temperatures near 0° C. and 36° C. Diemyctylus is indifferent to white light from above.
- 3. The above reactions are the same whether the light fall from above or come from below, though they are usually less marked in the latter case.
- 4. Diemyctylus is positively phototactic to lights of all intensities, from very weak daylight to an intense arc light.
- 5. At low temperatures this phototactic reaction is inhibited or reversed.
- 6. With an intense white light at each end of the aquarium the animals tend towards the less intense light; if neither light be of great intensity, perhaps not reaching a certain optimum, the animals tend towards the more intense light.
- 7. Phototactic reaction to pure red light was the same as to white light, possible a little more marked.

8. The reaction to green light is the same as to the red, but less marked.

9. The reaction to blue light is the same, but still less marked.

10. A small spot of white light from a micro-electric torch produced no effect when thrown upon various parts of the animal's body.

11. The animals responded promptly to a beam of sunlight thrown on various parts of the body, either from above or below, by a small mirror, though if the mirror threw a beam of 5 sq. mm. or less there was little or no response.

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ADDENDUM

As a check upon the preceding laboratory experiments, the following experiments were tried upon a number of newts of the same species, under as near natural conditions as could be obtained. The work was done, during the latter part of August. in a small, fresh-water pond, about two miles from the laboratory at Woods Hole, Mass.

Twenty-eight animals were obtained by sweeping a dip net through the grass of this shallow pond. They were caught during the morning, and were confined until night, and during intervals between experiments, in a 12 in. x 12 in. floating livebox, with wire top and bottom, which was partly filled with grass and dirt from the pond.

During experimentation they were confined in a cage 1 ft. x 2 ft. in area, 6 inches deep, and open above, made of one-quarter inch wire netting. This cage was sunk about 5 inches into the water so that it was surrounded by the grass of the pond. A few of the animals escaped, during the experiments, by climbing out of the cage.

Only sunlight and artificial white light were used, the latter being supplied by a miner's acetylene lamp with a reflector: this lamp gave a fairly brilliant though rather variable light, but its candle-power was not determined.

Experiment XXII.—This experiment was performed during a fairly dark, moonless night. One-half of the wire cage was covered with a board, while the other half was brilliantly illuminated by the acetylene lamp, fixed about 10 inches above the surface of the water. Fifteen observations, at 5-minute intervals, were taken, during which 65 animals were noted in the light half of the cage to 355 in the darkened half of the cage,—a proportion of more than five to one. This proportion would have been still greater but for the fact that after observations 2, 6 and 11 the light and dark ends were suddenly reversed, thus throwing the larger group of animals into the light area.

Experiment XXIII.—In this experiment the same cage and animals were used, but the light was bright sunlight. Of course, on account of the diffused light, the shaded half of the cage was not nearly so dark as in the preceding experiment. In 16 observations, at 5-minute intervals, 103 animals were counted in the light half of the cage to 297 in the dark; this proportion of nearly three to one would have been greater but for the sudden reversal of light and dark ends after observations 9 and 12.

It is evident, then, from experiments XXII and XXIII, that under these conditions the negative phototropism to white light is even more marked than in the-laboratory experiments.

Experiment XXIV.—In this experiment the acetylene light was placed in a large, glass aquarium jar, which was sunk into the water of the pond so that the light was thrown into one end of the wire cage, the observations being made, of course, at night. This arrangement was not very satisfactory, as the dark color of the pond-water made the illumination of the far end of the cage very dim.

In 26 observations, at 5-minute intervals, 213 animals were noted in the half of the cage nearer the light to 263 in the farther half. After observations 9, 20, and 22, since it was difficult to reverse the ends of the cage, all the animals were pushed into the light half; this tended to decrease the excess of those in the dark end; but the experiment was hardly conclusive, perhaps on account of the unsatisfactory conditions.

Experiment XXV.—This experiment was performed with the clear sun shining down upon the end of the submerged cage, at an angle varying from 40 to 25 with the surface of the pond.

The cage being uncovered, the light was evenly distributed over the bottom, but entered, as said, from one end. Under these conditions, in 16 observations, at 5-minute intervals, 191 animals were noted in the half of the cage towards the sun, to 120 animals in the other half. After observations 8, 11, and 14 all the animals were gently pushed to the center of the cage, which diminished the preponderance of those in the half towards the sun. This experiment seems to indicate that, where the light is sufficiently bright, the animals tend to go towards it, as in the laboratory experiments.

These outdoor experiments, then, seem to substantiate, so far as they go, the results of the laboratory experiments.

THE INTERFERENCE OF AUDITORY HABITS IN THE WHITE RAT

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The present paper has grown out of the work which one of the authors has already published on audition in the rat. On pages 324-5 of the last of these a report is made of some tests on the retention of auditory habits. It was these tests that gave us our cue. Negative results only had been secured by attempting to train rats to turn in one direction through a box when a tone or a chord was sounded and to turn in the opposite direction when silence was given. This was a direct attack upon the problem of tone sensitivity by the association method. It occurred to us that working indirectly through habit interference further data of value might be secured. By such a method one could redetermine whether for the rat certain tones are equivalent to silence. Should such a method succeed, its data would be similar to that secured by the conditioned reflex method: In the present paper we shall deal only with the tests bearing upon habit interference. An immediately succeeding article will stress the auditory sensitivity data secured by this method and combine them with other observations from this laboratory.

The same T-shaped discrimination box was used here that has been described in the previous papers. The buzzer was held on a wire over the apparatus in the same location indicated for the tuning forks. The initial plan (which was much supplemented as will be seen) called for 20 rats as follows:

A. 20 rats train to turn rt. for handclaps, lft. for silence.

B. 4 rats of set A train for 30 days to turn rt. for buzzer.

Hunter, Walter S. The auditory sensitivity of the white rat. *Journal Animal Behavior*, vol. 4, p. 215, 1914, and vol. 5, p. 312, 1915.

- C. 4 rats of set A train for 30 days to turn rt. for tuning fork 256 d. v.
- D. 4 rats of set A train for 30 days to turn lft. for tuning fork 256 d. v.
- E. 4 rats of set A train for 30 days on regular series of presentations on auditory stimulus.
- F. 4 rats of set A tested for retention after 30 days rest.
- G. Rats of sets B, C, D, E retested on handicaps.

This program calls for a measure of the relative retention of a simple co-ordination in five groups of animals, each group having been kept under different conditions for an interval of thirty days.

Only 18 rats completed the work of set A. Of these 13 were females (numbers 1, 4, 9, 10, 11, 14, 15, 16, 18, 19, 20, 21, 24), and 5 were females (numbers 7, 8, 17, 22, 23). All were about three months old at the beginning of the tests. With the exception of nos. 1 and 4, they were untrained. No. 1 had been trained on the inclined plane problem box. No. 4 had worked with light in a two-choice discrimination box. Nos. a, b, c, 25, 26, 27, 28, 29, whose records are given below, were also about three months old at the beginning of the tests. All of these animals were females. The tests here reported, like most studies of animal learning, have been long and tedious. They have extended from January, 1915, to June, 1916.

Prior to the regular tests, each rat was fed on the experiment table and was permitted to run through the box on each of two days. Care was taken that no position habits were developed. Those rats that manifested a preference for a certain side of the box were immediately forced through the opposite side.

Discrimination was regarded as established when the average percentage of correct reactions for four days together was $87\frac{1}{2}\%_0$ with no one day's record below $80\%_0$.

II

Learning the first habit.—Table 1 gives the total number of trials required by each rat to set up the habit of running to the right for handelaps and to the left for silence. The period of learning is the period up to the 40 trials made at the standard per cent. The rats underscored are males. Figure 1 shows

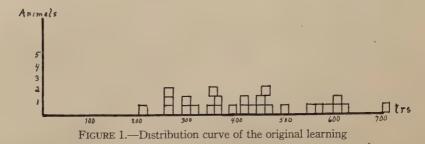
the distribution curve. All but six of the rats had mastered the problem within 500 trials. I am inclined to attribute the irregularities largely to position habits which appeared during the learning and which had to be overcome. Fear caused by punishment retarded the last part of the learning in rats 25-29. No sex differences appear. The form of the learning curve will be shown in section VIII.

TABLE 1 Number of Trials per Rat in Learning First Habit

Rat	Trials	Rat	Trials	Rat	Trials
1	260	16	260	a	350
$\overline{4}$	210	17	300	b	420
7	430	18	450	c ·	460
8	500	19	450 .	25	420
9	300	20	710	26	550
10	390	21	610	27	320
11	370	22	620	28	610
14	370	$\overline{23}$	470	29	570
15	360	$\overline{24}$	260		

Each rat of set A, when it had completed its four days with a general average of $87\frac{1}{2}\%$, was given three controls, each of which in general alternated with a day on the normal stimulus of handclaps. Control 1—no stimulus was given. The reaction was counted correct if it agreed with the series of presentations. This control was to test the animal's dependence upon extra-auditory cues. Control 2—an electric buzzer was sounded in place of the handclaps. This control was given to each rat on each of four successive days (40 trials). Control 3—a tuning fork, 256 d. v., placed over the apparatus as described in previous papers, was sounded by striking with a felt hammer. This tone was substituted by the experimenter for the handclaps. The necessity for the first control needs no comment. Controls 2 and 3 were used in order to determine the relation of the respective stimuli to the habit just established. It is very important, if interference effects are to be studied, that the mutual relations of the stimuli (i.e., their transfer relations) be known, in the present case, whether the buzzer and the tuning fork would be substituted readily for the handclapping in this particular co-ordination.

The results of control 1 indicate that the animals were depending upon auditory cues. Only one rat's (No. 17) record was



the least ambiguous. The accompanying table (No. 2), however, will show that an extended use of the control produced low percentages. Control 2, where the buzzer was substituted, gave the following results: On the first day, 7 rats (Nos. 15, 18, 20, 22, 9, 10, 11) made below 80%. On the second day, 5 rats (Nos. 20, 22, 10, 11, 14) made below 80%. On the third day, 3 rats (Nos. 21, 8, 11) made below 80%. On the fourth day, Nos. 9 and 14 fell below 80%. Seven rats (Nos. 1, 4, 7, 16, 17, 19, 23) never fell below 80%. The adjustment or transfer was thus usually made either at once or by the end of the second day. On control 3, 6 rats at different times made a day's record with 80% correct. This occurred, however, with a majority of days at 50, 60 and 70% and is to be regarded not as evidence of auditory sensitivity, but as an accident in the grouping of kinaesthetic factors.

TABLE 2:
RECORDS ON CONTROLS GIVING CORRECT CHOICES OUT OF 10
The text states that not all records are from successive days

			•
Rat	Con. 1	- Con. 2	Con. 3
15	6, 5, 6	5, 10, 8, 8	. 7, 6, 7
16	7, 4, 5	8, 9, 10, 8	6, 6, 8, 6
17	8, 5, 7, 8, 6, 5	8, 9, 8, 9	8, 7, 7, 10, 7, 7
18	5, 6, 6	6, 8, 9, 10	8, 9, 5, 8, 5
19	4, 5, 7	10, 10, 9, 9	6, 7, 8, 7
20	6, 6, 6	7, 5, 10, 9	6, 6, 5
21	6, 6, 5	9, 9, 6, 9	7, 6, 7
22	6, 5, 5	7, 6, 8, 10	6, 7, 4
	5, 5, 7	8, 8, 9, 9	7, 8, 7, 7
23 1 4 7 8 9	6, 5, 6	10, 8	6, 5, 5
4	6, 7, 5	9, 10, 8, 9	6, 7, 5
7	7, 7, 6	9, 10, 8, 8	5, 7, 7
8	5, 6, 6	9, 8, 7, 8	6, 6, 7
ğ	6, 6, 6	6, 8, 9, 6	5, 6, 5
10	6, 3, 4	7, 5, 8, 10	7, 6, 6
11	5, 3, 5	7, 5, 6, 9	
14	6, 5, 6		7, 6, 8, 6
14	0, 0, 0	8, 7, 9, 6	5, 6, 7

Table 2 presents the results for these controls. The four days' records preceding control 1 were made at or above $87\frac{1}{2}\%$ correct. Each day's record with controls 1 and 3 alternated with a day on the normal stimulus (handclaps) save when 80% was made. In these cases the same control was used on the succeeding day.

TIT

Thirty-day Tests.—After control 3 had been given, each rat of set A received the normal stimulus for four days or until the standard 87½% was reached. The animals were now started upon the interference periods (B-E) as outlined above for 300 trials or 30 days. No rat learned his problem within this period. Only one rat (No. 15) made 80% during any one-sixth (50 trials) of the period. This rat made 82% during the third 50 and 84% during the fourth 50 trials. (These are general averages for the 50 trials.) After this he broke down, so that on the final sixth 50% only was made. There is no available explanation for this. Neither fear nor position habits intervened. It is one of those anomalous cases that will occur. (It took this rat 180 trials to relearn the normal habit. This, however, cannot be correlated with the high percentage in the interference period because long periods of relearning appeared in other rats where the high percentages were absent.) Each of the succeeding 50 trials for the rats in these sets averaged practically between 50 and 65%. Table 3 contains a record of the number of correct reactions in each 50 trials made by each rat during the 30 days.

TABLE 3

TRIALS CORRECT IN EACH 50 DURING THE 30-DAY TEST AND THE RELEARNING 30-day training

Sets		В			C		. !		E)			E			F		
Rats	15	23	7	11	1	17	18	16	14	10	20	9	19	21	4	24	8	22
	28 32 41 42 31 25	31 34 29 33 17 28	13 19 23 26 24 27	20 25 24 30 19 20	28 26 23 20 27 23	32 27 26 31 21 29	29 27 24 26 28 24	35 43 34 33 35 33	29 33 33 35 26 28	27 26 35 27 32 28	26 32 24 26 29 29	24 24 27 25 30 29	28 28 30 33 28 27	14 15 19 21 21 19				

Re	102	ורייוו	111	3
TIL	100	11 11	111	54

		1				-							1			
36	35	24	46	37	38	35	38	39	44	35	34	37	45	37	45	33
33	of	36		42	37	10			10	of	of	of	9	of		37
41	40	of		41	35	of		40	of	40	40	40	of	40		40
39		40		9	37	10			10				10			42
9				of	40											41
of				10	18											16
10					of											of
					20											20

Total trials on relearning

On the day following the close of the 30-day period each rat was retested on handclaps to the right. The results are included in table 3. Our criterion of the degree of retention has been the length of the period of relearning rather than the per cent of correct reactions on the first day. Table 4 shows that in the present case there is no way of predicting the amount of relearning from the percentages made on the first days. It will be seen from table 3 that all sets of rats are essentially on a par with respect to retention. In other words, so far as these rats are concerned, 30 days of diverse training has not produced effects in retention.

TABLE 4

F stands for number of trials correct in first 10 of relearning. T is the total relearning time in trials.

	В			С			D			E			F	
Rat	F	T	Rat	F	T	Rat	F	T	Rat	F	T	Rat	F	T
7 15 23		90 210 40	11	5 10 7 2	60 50 270 160		8 10 8 8	40 40 50 40	9 19 21	7 9 9	40 40 60	4 8 22 24	9 7 2 7	40 270 130 50

IV

Sixty-day Rats.—Four rats (Nos. 1, 11, 17, 18) had been tested in the work outlined above. During the 30-day period an effort was made to train them to turn right for the tuning fork 256 d. v. without success. These rats were then idle, al-

though kept in good physical condition, for the following intervals of time: Nos. 1 and 11 went 10 days; No. 17 went 23 days; and No. 18 went 40 days. At the close of these intervals of time, all of the rats were brought back to the standard percentage of correct reactions on turning to the right for handclaps. They were then put into training again on going right for 256 d. v. and left for silence. They remained in this series for 600 trials, 10 per day, punishment and reward. No. 11 was the only rat of the four that improved during the 60 days. He learned the reaction in 270 trials. The senior author was away for the summer at this time and no control tests were made to determine the basis of the response. Inasmuch, however, as no other rat in the laboratory has learned to react to tone in this fashion since the work was begun in 1913, and inasmuch as this rat learned rapidly, it is most probable that the reaction was due to secondary cues accompanying the tone. This experiment is confirmatory of work previously published indicating the insensitivity of the rat to certain tones.

At the close of the 600 trials, retention tests for handclaps to the right were given. No. 1 came back to standard in 10 trials; No. 17, in 60; and No. 18, in 30. This is practically perfect retention and is as good a record as that made by the 30-day rats. The results are practically comparable, although not absolutely so inasmuch as the 60-day animals were somewhat overtrained relatively on h. c. to the right.

The same results with the same limitations were secured with rats 4, 8, 22 and 24. These were the rats listed under F in the 30-day tests. The retention tests in that series brought these animals back to the standard. They were then idle for 60 days at the close of which period they were again retested on h. c. to the right. Rat No. 4 came back to standard in 20 trials; No. 8, immediately; No. 22, in 30 trials; and No. 24, in 40. In order to compare the results given here and in the above paragraph with those listed under "Total trials on relearning" in table 3, it is necessary to subtract 40 from each of the totals in that table. The results given in the present section are the number of trials up to the 40 made at the standard per cent.

Rats Nos. 7, 15 and 23 had been through the 30-day tests in set B,—turn left for the buzzer. After intervals of rest as

follows they were brought back to standard on handclaps: No. 7, 9 days; No. 15, 38 days; and No. 23, 47 days. They were now retrained on going to the left for the buzzer and to the right for silence. The intention was to train them upon this for 60 days, unless the habit was established sooner, and then test their retention of h. c. to the right. Rat No. 7 learned in 54 days, 540 trials; No. 23 learned in 35 days, 350 trials; and No. 15 learned in 45 days, 450 trials. If we add to this only the 300 trials which they had previously had on the same problem in the 30-day test, No. 7 learned in 840 trials; No. 15, in 750 trials; and No. 23, in 650 trials.

At the close of the 40 trials at the standard percentage for rats 7, 15 and 23 as just noted, they were retested on h. c. to the right. No one of the three fell below 80% for 30 trials. In other words, there was perfect retention. When given control 1—tests made without the auditory stimulus—the percentages ranged between 30 and 50. On one day and with only one rat did it go as high as 70%. So there could be no doubt that the rats were dependent upon the auditory stimulus. Here we have a case where two opposite habits are present simultaneously in the organism although the respective stimuli were not originally differentiated. The process of the differentiation has been a successive formation of habits and not a simultaneous one as is usual in discrimination tests. And the interesting thing is that the formation of the second (and opposite) habit has not interfered with the retention of the first habit. A second automatism has arisen gradually and independently of the first.

Further tests were made upon rat No. 7 to determine the nature of the difference between the buzzer and the handclaps. These results will be published in a separate paper.

V

Ninety-day Rats.—Three untrained rats, Nos. a, b and c, were trained to go right for handclaps and left for silence. The number of trials required in learning is shown in table 1. At the close of this series, control 1 was alternated with normal for three days in order to be sure that the animals were not depending upon extra-auditory cues. The percentages were all around 50. These three rats were then given a period of idleness for 90 days. During this period, they remained in

splendid physical condition for experimentation. At the close of the period, they were retested on h. c. to the right. It is needless to give the data in detail. No one of these rats averaged above 70% for any 50 trials although their retraining extended through from 34 to 45 days. Their behavior at the beginning of the retesting indicated that the apparatus and method were still familiar to them, but that was all. The results as a whole indicate that these rats had lost all measurable traces of the original training. It may be well that in a habit so difficult as the present one continued or retained familiarity is too slight an aid to manifest itself in shortening the period of relearning. The disintegration of this habit in the white rat apparently takes place between 60 and 90 days. The 60day tests indicated practically perfect retention at the close of that period, but the two sets of data are not strictly comparable. The rats in the 60-day tests had been retrained at different intervals on h. c. to the right after the original learning. Hence the habit was considerably overlearned.

VI

Effect on retention of learned vs. unlearned habits.—It would be interesting to know just what went on in the rats' nervous systems during the 30 and 60-day periods of training. We seem forced to assume that certain synaptic connections have persisted in spite of the attempts of incoming stimuli to disintegrate them. Inasmuch as either continued training (?) or the lapse of time will result in the disintegration of these connections, definite problems arise under each condition. We have indicated that with the mere lapse of time, the dissolution of the particular habit in our rats occurred between 60 and 90 days. The present section contributes data throwing light upon the comparative disintegrations brought about in the h. c. habit by the 30 days' ineffective training on B and by a period of training during which B was mastered.

Of the 18 rats used on the 30-day test described above, 9 made the standard $87\frac{1}{2}\%$ immediately upon being re-tested on h. c. to the right. Four others did essentially as well. Two hundred and seventy trials was the maximum period of relearning and was found in two rats. Table 3 gave the data in

detail. It will also be recalled that no one of these rats im-

proved during his 30-days' training upon B.

Three untrained rats, Nos. 26, 27 and 29, formed the original h. c. habit as indicated in table 1. They were then trained on B until it was mastered. (I shall discuss certain details of this training in a following section.) At the close of the 4 days on B made at $87\frac{1}{2}\%$, these rats were retested on h. c. The results for all save the original learning are given in table 5.

TABLE 5

Correct in successive 50 trials in learning B

No. 25	No. 26	No. 27	No. 29
14	15	. 15	5
10	15	19	20
18	20	22	18
17	12	38	21
18	22	36	21
19	$\begin{array}{c} 21 \\ 22 \end{array}$. 33	19
20	22	30	17
22	20	34	. 24
25	29 .	33	32
28	32	38	36
28	37	34	29
30	37	36	31
29	34	$3\overline{2}$	34
31	38	. 38	35
34	. 39	38	36
34	37	15 of 20	39
$4\overline{2}$	38	10 01 20	32
Unfinished	32		
Chimished			41
	7 of 10		13 of 20

Correct in each 50 in retest on h. c.

29	36	26
31	36	35
30	32	24
31	33	33
36 .	38	34
24 of 30	41	8 of 10
	8 of 10	

No 26 required 280 trials for the re-learning here in question. No. 27 required 310; and No. 29, 260 trials. The intervals for 26 and 29 are a little too small inasmuch as these two rats grew sick and died. Each, however, had reached 80% correct and so was within $7\frac{1}{2}\%$ of the standard. The indications from this test are that marked progress must be made in the formation of a second contradictory habit before the retention of a first habit is noticeably affected. This can be represented graph-

ically as indicated in figure 2. The three lines to the left are based upon rats 26, 27 and 29. The three lines to the right are based upon the 18 rats of the 30-day test. The first line in each column represents the average number of trials in learning the original h. c. habit; the second line, the trials given on habit B; and the third line, the re-learning time. The detailed data have already been given in the tables. The rats represented in the right hand column averaged about 5 months old at the beginning of the relearning tests. This was approximately 2 months younger than the other set of animals at the corresponding point of their tests. Both sets were composed

FIGURE 2.—Effects on retention of learned vs. unlearned habits.

of active animals, however, and in view of the marked difference in results as compared with Hubbert's, I am inclined to discount age as an important factor in determining the present data.

A comparison between these data and the results of the 90day test points the way toward interesting interpretations. The 90-day rats had lost all measurable traces of the original h. c. habit whereas rats 26, 27 and 29 relearned within an average of 260 trials or 26 days. These three rats had spent 85 days on habit B. Unless these are accidental variations, then, it would seem that the training on B favored the retention of h. c. The rats seemed equal in physical fitness for the tests. If we now consider the relations of the data given in figure 1, it would seem that the loss in retention of the first habit is probably caused as much or more by the lapse of time than by the formation of the contradictory habit. It was found in the 30-day test that training had no greater effect on retention than lack of training. It is thus suggested, although not clearly proved by our tests, that the disintegration of certain habits in the rat is due to a temporal factor and not to habit interference.

² Hubbert, H. B. The effect of age on habit formation in the albino rat. Behavior Monographs, 2, no. 6, 1915.

VII

The Strength of Habit.—Rats 25, 26, 27, 28 and 29, whose learning periods were described in the first section of the paper, were further tested as follows: At the close of the 40 trials at $87\frac{1}{2}\%$ made on the first h. c. habit, each rat was given control 1 on three days alternating with the normal. All of the rats failed to respond correctly in this control. They were then each given two consecutive days on control 2 (buzzer substituted for h. c.). In case a rat fell below 80%, a day with the normal stimulus was interpolated. The results are in table 6.

TABLE 6

	No. 25	No. 26	No. 27	No. 28	No. 29
Н. С	9	10	9	. 8	8
Con. 2	8	6	9	8	3
H. C		8 .			8
Con. 2	9	7	8	,	8
Con. 2		• <u>•</u>	8		• •
H. C		7			8
		8			

It will be seen from this that rat 26 did not rate the buzzer as identical with the handclaps and that No. 29 failed also, but on the first day only. No 28 became sick on the third day and was dropped from the tests. At the close of the tests in the above table, Nos. 25, 26, 27 and 29 were immediately started on learning "buzzer to left, right for silence" which was the opposite habit to the extent shown in the table. The progress of learning B in successive fifties was shown in table 5. The very important point that I wish to emphasize is that no one of these four rats learned in less than 770 trials while two were as high as 910 and 920. It took these rats approximately twice as long to break the h. c. habit as it had to form it. The figures are: No. 25, h. c. habit-420, buzzer habit-850 (?); No. 26, h. c. habit-550, buzzer habit-910; No. 27, h. c. habit-320, buzzer habit-770; No. 29, h. c. habit-570, buzzer habit-920. These figures exhibit in a striking manner the tenacity of habits in the rat. The original habit need not be literally broken, however, because in each case a period of retraining reinstated it. The situation is probably more accurately described by saying that the first h. c. habit interfered with the formation of the buzzer habit, although the latter but slightly (if at all) affected

the former. The amount of the interference will probably depend much upon the ease of discrimination between the stimuli for the two habits. We are not prepared to contribute upon this point. (Because the rats ranked the buzzer as the same as handclaps we have felt justified in assuming that untrained rats would learn "buzzer to the left" as readily as "hand claps to the right.")

Mrs. Binnie Pearce, in research from this laboratory as yet unpublished, found even more striking interference in visual habits. Using the same T-shaped box, she trained rats to run one way for light and the other way for darkness. When she then attempted to train them to reverse this behavior, the task was found all but impossible.

We are not familiar with any other work where an animal has had to learn the opposite of a previously acquired habit. There are many cases where different habits have been set up in succession and where interference has been more or less explicit. However, in order to secure comparable data, it is necessarv that the stimuli be known and the responses simple. The study of interference in mazes, latch boxes, etc., suffers for this reason. Not only must the stimulus be known in the case of the first habit, but the second stimulus must be known physically and also physiologically in terms of the first one. Thus one can know whether or not the stimulus for the second habit is for the subject in that situation the same as the first stimulus (positive transfer). Where the type of habit set up is kinaesthetic as opposed to auditory or visual, the control of the stimulus is very difficult because the stimulus lies in the animal's movements. The most feasible procedure is to reduce the problem to such an extent that only one or two prominent kinaesthetic experiences are presented. The senior author is working upon this problem at the present time, although interference is but one phase of the study.

VIII

Relative rates of error elimination in interfering habits.—With particular reference to the 30-day rats and rats 25-29, it is of interest to raise the following question: In what parts of the learning curves does the interference, as measured by the relative rates of error elimination, occur?

Table 7 gives data for rats 25, 26, 27 and 29. The numbers represent the percentages correct in each succeeding one-tenth of the learning process.³ The first columns for each rat are

TABLE 7

25	26	27	29	Av.
50 23	54 29	50 31	50 23	51 26
57 34	63 29	50 45	70 39	60 36
57 37	38 35	43 75	64 42	50 47
57 38	60 45	59 64	68 35	50 45
78 50	54 49	43 64	61 58	59 55
66 53	72 67	59 70	64 64	65 63
64 60	61 71	75 68	70 64	67 65
59 59	76 73	65 71	77 69	69 68
59 68	76 75	75 71	82 82	73 74
78 76	74 71	81 75	66 75	74 74
87.5 90	87.5 87.5	90 87.5	90 90	88 88

the records for learning the original h. c. habit. The second columns are the records for learning B. These figures are secured as follows: No. 25, e.g., learned h. c. in 420 trials. This is divided into 10 parts of 42 each. Of the first 42, 21 or 50% were correct. This method when applied to all members of the group enables us to construct a curve which throughout its length is representative of the group. The bottom numbers in each column of table 7 represent the percentages of correct reactions made in the last 40 trials. Sometimes this runs over the standard 87.5%. The values above S are from the forties made at or above the standard per cent.

If the curves of figure 3 are examined, the curve for B is seen to start much lower than the curve for h. c. and to lag markedly behind throughout eight-tenths of the learning. (These curves are plotted from the average values in table 7.) This lag would be even greater, but for the accidental fact that learning h. c. was retarded toward the last by the fear that arose in the rats from punishment. The marked interference of the two habits is seen when the last of h. c. is compared with the first of B, and also when the first parts of the curves are compared. B is more than a new habit. It is interfered with from the start by h. c.

³ This method of treating the learning process is taken from Dr. S. B. Vincent's Function of the vibrissae in the behavior of the white rat. Behavior Monographs, 1, no. 5, p. 17, 1912.

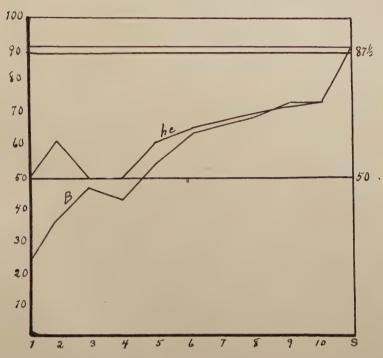


FIGURE 3.—The relative rates of error elimination in the hand clapping habit and the buzzer habit. Based on rats 25, 26, 27 and 29.

TABLE 8

15	23	7	Av.	
52 57	57 48	39 46	49 50	
52 57	61 65	48 50	53 55	
61 64	61 60	51 48	57 57	
36 55	70 65	55 53	53 57	
63 68	59 54	62 48	61 56	
63 75	59 54	69 57	63 62	
80 55	76 57	83 51	79 52	
88 71	76 68	67 55	77 64	
83 75	72 65	86 59	80 66	
66 71	78 51	67 61	70 61	
95 90	90 90	87.5 90	90 90	

Table 8 gives data for rats 15, 23 and 7, used in set B of the 30 and 60-day tests. In this table again the first columns are the original learnings; the last columns, the learnings of B in the

60-day test. These rats had received 300 trials in the 30-day test followed by some intermediate training on h. c. If this data were included in the curves, there would be no variation in their essential relations. If anything the interference would be more apparent.

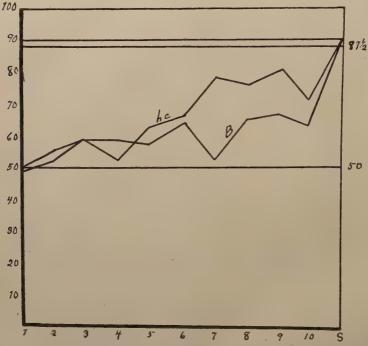


Figure 4.—Relative rates of error elimination in h. c. and in B. Based on rats 15, 23 and 7

The curves in figure 4 begin at essentially the same height and go along together throughout the first six-tenths of the learning. It is during the last four-tenths of the curves that the B-curve remains markedly below that for h. c. (There is no evidence that this was caused by fear.) The interference of the two habits is seen here and in a comparison of the last of h. c. and the first of B. In the average B is no more than a new habit with these rats. Its curve begins no lower than that for h. c. The details are further brought out in table 9, which gives the correct responses in each 10 trials of the first

100 trials of the 30-day test with B. It will be seen from this table that there is no essential difference between the initial stages of the two habits.

TABLE 9

 7		15		23	
h. c.	В.	h. c.	В.	h. c.	В
5335244763	3 2 2 2 4 4 5 6 1 3	73656735499	3578555778	3 7 5 10 5 8 4 6 6 5	4 6 5 8 8 7 6 8 6 7

IX

Conclusions.—The present paper opens up problems in an all but unexplored field of animal behavior. Keeping in mind the limitations imposed by the number of animals and the type of experiment, the following conclusions may be stated as the more important ones to which our work points:

- 1. Habit interference occurs in the white rat between a first habit and the formation of a second one.
- 2. This interference may or may not manifest itself at the beginning of the second habit and may or may not manifest itself later during the second learning.
- 3. "Interference" is most marked between the end of the perfected habit and the beginning of the new habit. In many cases this may show not genuine interference, but merely the beginning of a new habit.
- 4. Habit interference may serve greatly to slow up the formation of a new habit. Clear evidence of this forward reference has been found. We have brought to light no evidence that learning the second habit as such interferes with the retention of the first habit.
- 5. It seems clear that in some cases the lapse of time may be more effective than intervening training in disintegrating a habit.

THE CRITERION OF LEARNING IN EXPERIMENTS WITH THE MAZE

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In comparative studies of the rate of learning in which animals are trained in the maze the selection of a proper criterion by which to judge the progress of habit-formation in different groups of animals offers a rather difficult problem. There can be little doubt that the ability to thread the maze without error is the final test of learning, but whether a single trial without error, three successive trials as used by Hubbert, or a still larger number of errorless runs should be required before the habit is considered as established has so far been determined largely by the convenience of the experimenter. The question is chiefly one of economy of the experimenter's time, but not wholly so, for, although all animals may become automatic in running the maze after long training, an occasional error still appears and no method of evaluating these has been devised.

In some tests dealing with the effects of drugs upon the rate of learning I have recently trained 94 rats in the Watson circular maze, obtaining data which makes possible a limited comparison of such criteria of learning.

The animals were all given five trials per day in the maze with food at the end of each trial. At the beginning of the experiments, as an arbitrary standard of "perfect learning," a single record of three successive errorless trials on the same day was selected. After this degree of proficiency is once attained the animals make very few errors, so that this standard actually represents very nearly the limit of training, but it was chosen simply because it could be attained after about ten days' training.

To test the reliability of this standard in estimations of the difference beween groups of animals its results have been compared with those of another standard, that of the number of trials preceding the first which was made without error. comparison is best made by correlating the number of trials preceding the first errorless run with the number preceding 'perfect learning" for all the animals. The former varied from 10 to 75 with a mean at 23.8±.977, the latter from 10 to 150 with the mean at 47.3 ± 2.99 ; the correlation in the variations of the two is 0.632+0.061. The coefficient of regression of the variations in trials preceding the first errorless run over those preceding "perfect learning" is 1.304, that of variations in "perfect learning" over first trial is .306. This means that if we are dealing with fairly large numbers of animals and have found a given difference between two groups, as measured by the average number of trials required to make one perfect run, we may expect that the difference in the number of trials required for "perfect learning" will be in the same direction and 1.304 times as great. Conversely, if we know the difference in trials required for "perfect learning" we may predict a difference .306 times as great in the number of trials required for one error-

It follows from this correlation that that group of animals which has made the most rapid progress up to the time when the first errorless run is made will continue in the lead until the limits of training are reached; will, indeed, increase that lead. As a test of the application of this principle, the groups of animals which were treated differentially in the experiments have been graded in the order of the average number of trials required by them to attain to each of the two standards. The results of this are shown in table 1. The different methods of rating result in an interchange in the order of some of the groups but in no case is the position of any one group changed by more than one place.

The groups included in the table are not all strictly comparable. The methods of training were the same in every case but some of the groups differed in the heredity and age of their members, in the season during which they were trained, as well as in certain drugs administration during training. In the separate experiments, all these factors were controlled and the groups a, f, g, and i, c, and d and b, e, h, and j are mutually comparable and differ only in the drugs administered. The order of these by the two criteria of learning is—

The order is changed in this case only between the groups f and g, and the difference between them is not great enough to be significant in either case. There is essential agreement in the results obtained by the two criteria.

As will be noted in the table and from the coefficients of regression, the difference between the groups is greatest when measured by the difficult standard of three perfect trials.1 Are these differences more significant on this account? At first sight it might seem so. The number of animals considered remains constant and hence, other things being equal, the ratio of the difference to its probable error increases. But the probable errors are dependent also upon the amount of variability and a further analysis of the data shows that the coefficient of variation remains constant or is even increased when the more difficult standard is used. The figures in table 2, which are taken from groups c and d, illustrate this. The probability that the first difference in the table (3.54) is due merely to chance is about 1/3; that the second (4.12) is due to chance is 1/1 or greater. A glance at the probable errors for the averages of all the rats (page 70) shows that these are quite consistent with the results for the smaller groups.² The coefficient of variation in the number of trials preceeding the first errorless run is .5900, for those preceeding "perfect learning" is .6107 and the probable error of the average of the latter is proportionately greater than that of the former. If two such groups were compared by the two criteria the differences obtained would obviously bear the same relation to their probable errors as do those in the smaller groups.

The general results of this analysis point to the following conclusions: 1. Where there is a difference in the average capacity of two groups of animals for habit-formation, the more difficult the problem that they are required to learn the greater will be the apparent difference between the groups in the practice re-

¹ Some exceptions occur, but this is to be expected from the small number of

animals included in the groups.

² No great importance could be ascribed to this fact alone as it does not follow that there is any correlation between the variability within the subordinate groups and the variability of all the animals taken together, but the fact that the same results are obtained for both the small and large groups does seem significant.

quired for learning. 2. With the increasing difficulty of the problem there is an increase in the extent of variation between the members of the same group so that the greater difference between the groups looses its significance through the increase in the probability of chance variation of the averages. 3. Hence there is no advantage, for reliability of results, in prolonged training where the problem is that of a statistical comparison of different groups of animals by a single standard of achievement.

These conclusions apply only to a specific technique, but one which has been used extensively in studies of the effect of age. sex, distribution of practice, etc., upon the rate of learning. It may be argued that long training permits the comparative study of the rate of learning at different stages of proficiency. This is quite true, but the analysis of learning curves based upon the averages of several animals has contributed remarkably little to our knowledge of the mechanism of learning and in statistical studies of the sort under discussion there is not time for that detailed analysis of the individual behavior of the subjects which is of value in the interpretation of the form of the learning curve. On the other hand the results of studies of the modifiability of the course of learning by environmental factors are for the most part questionable because of the small number of cases upon which they are based. In many cases differences which are smaller than their probable errors have been regarded as significant, seemingly only because they support the hypothese of the writers.

The use of an adequate number of animals is difficult for the reason that the groups to be compared should be trained at the same time to rule out possible seasonal differences, of which we know nothing at present, while only a limited number of animals can be trained by one man at one time. A possible solution of the difficulty is the cooperation of several students upon a single problem but there is not enough data upon the influence of the experimenter's personal equation to permit of this as yet.³ The alternative seems to be the simplification of

³ The use of two or more criteria as in the experiments reported, while reducing the probable errors of the average difference found, removes hereditary and like individual differences from the category of chance variations and places them on an equal footing with the experimental differences (age, sex, or whatever difference is being studied) as the cause of the diverse rates of learning revealed by the experiments.

the problems presented to the animals so that a greater number may be trained. If the evidence given above can be verified by more extensive data this solution will doubtless prove to be the most satisfactory.

TABLE 1

The average number of trials required by differentially treated groups before reaching the standards described in the text. The number of animals from which the averages were taken is given at the left and the relative rating of the groups by the two standards on the right.

Group	Number of animals	Trials preceeding "perfect learning"	Trials preceeding 1st perfect runs	Rating by "P. L."	Rating by 1st P. R.
a b c d e f g h	9 6 16 16 6 10 10 6 9 6	24.5 30.0 31.0 35.2 42.5 43.5 48.6 65.3 74.4 82.6	14.8 14.3 16.6 19.6 18.0 23.0 20.4 31.3 32.4 43.0	1 2 3* 4 5 6 7 8 9	2 1 3 5 4 7 6 8 9

TABLE 2 Differences between groups c and d as measured by the two criteria of learning

Group		ls preceding errorless rui		Trials preceding three successive errorless runs			
•	Mean	Probable error	Coef. of Var.	Mean	Probable error	Coef. of Var.	
d c	19.60 16.06	1.480	. 448 . 622	35.12 31.00	5.922 2.428	1.000	
Difference	3.54±2.263			4.12±6.40			

THE REACTIONS OF DROSOPHILA AMPELOPHILA LOEW TO GRAVITY, CENTRIFUGATION, AND AIR CURRENTS

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Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy at Harvard College

No. 288

INTRODUCTION

Geotropism is characteristic of many animals and is often closely correlated with equilibration. The ear in vertebrates and the statocysts in invertebrates are evidently concerned with this reaction. In insects, however, there are no semi-circular canals or statocysts and it has not been proved that the so-called "static" organs (chordotonal, etc.) have to do with geotropism. Some other explanation is therefore to be sought. The experiments here described were carried out with the common fruitfly, Drosophila ampelophila Loew, for the purpose of determining (1) whether or not it is negatively geotropic; (2) how it responds to centrifugation and air currents; and (3) what mechanism can control these responses.

Carpenter ('05) concluded that gravity acted on Drosophila as a "directive" stimulus only, some "kinetic" stimulation, such as photic or mechanical, being necessary to induce locomotion. If this is true, how will Drosophila react to centrifugal force and air currents under conditions where light and mechanical stimuli are not effective? This question was suggested by the fact that the flies, without mechanical stimulation, were found to respond negatively to gravity in the dark as well as in the light. If it should be found that Drosophila reacts negatively to centrifugation or to air currents, then it would seem that gravity is a kinetic stimulus as well as a directive one. Another question closely related with this one, which must be considered is, by what means is the stimulus of gravity received?

The work was done under the direction of Professor G. H. Parker, to whom I wish to express my sincere thanks for guidance and suggestions throughout its progress.

EXPERIMENTS

1. Effect of gravity in the dark.—The first experiments were carried out in a dark box modelled after the one described by Carpenter, except that no heat screen was used. The glass cylinder employed was 18 cm. long and 4 cm. in diameter, and was marked off by fine ink lines into six regions of equal length, to facilitate locating the flies at the end of the experiments. A small number of flies were put into the cylinder and attracted to the top end by a strong light. Quickly but carefully the cylinder was placed, this end down, inside the box. After a period of one minute the door was opened, the lights turned on and the position of the flies noted. Observations were also made with a single animal, with smaller and larger cylinders of celluloid as well as of glass, but since the results were always the same it is not necessary to describe these modifications in detail.

The results of 58 trials involving 26 different animals showed that an average of 82 per cent went to the uppermost third of the cylinder after it was inverted, that 4.8 per cent remained in the lowest third and that the others stopped creeping in the middle third. The individual readings for those at the top varied from 67 to 92 per cent. In other words the animals reacted negatively to the stimulus of gravity in the dark. Whether or not this response is due entirely to gravity without regard to the mechanical stimulus of turning them over will be considered later.

One of the sets of records in this series of experiments is given in Table I.

2. Effect of gravity on flies equally illuminated from above and below.—The dark box was converted into a light box by the introduction of two electric lights, one at each end. These were either carbon-filament lamps of 16 candle power or 15-watt Mazda lamps. As before, the flies were attracted to the top of the cylinder, which was then inverted and placed in the light box.

¹ Carpenter's heat screen, because of the thinness of the water layer, was probably of no great value in preventing the action of the heat on the flies.

TABLE I

Showing the position of 5 flies in 14 trials, after having been in the dark box one minute. At the beginning all the flies were in section 6. 85.71 per cent crept to the uppermost third of the cylinder (sections 1 and 2).

NUMBER OF FLIES IN THE DIFFERENT SECTIONS OF CYLINDER

Trial number.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	Total
Section 1	5	4	3	4	4	3	4	4	5	3	2	3	3	4	51
Section 2		1	1			1				1	2	1	2		9
Section 3				1			1			1	1	1			5
Section 4			1		1	1		1						1	5
Section 5															0
Section 6															0

After one minute the readings were taken. Eighty per cent of the flies used in 50 trials went to the top section, 9 per cent remained at the bottom and 11 per cent went to the middle. Here also the flies responded negatively to gravity.

A set of records from this series is given in Table II.

TABLE II

Showing the position of 5 flies in 14 trials after having been one minute in the light box with equal illumination at top and bottom. 78.57 per cent crept to the uppermost thirdr

Number of Flies in the Different Sections of Cylinder

Trial number.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	Total
Section 1	3	5	5	2	3	5	3	3	2	4	1	3	2	1	42
Section 2				2	1		2	1	1	1	1	1	1	2	13
Section 3	1												1	2	4
Section 4	1			1					1			1			4
Section 5					1			1	1		3		1		7
Section 6															

3. Effect of gravity on flies illuminated either from above or below.—In order to study the effect of unequal illumination, a

single lamp was used either at the top or the bottom. When the top lamp was lighted 98.5 per cent of the flies went to the top after one minute, the others reaching the middle section. Twenty trials with 12 different animals were made.

With illumination from below 70 trials on 21 flies resulted in 61 per cent going to the uppermost third and 22.5 per cent remaining in the lowest third. Thus when light acts contrary to gravity a smaller number of flies are found at the top. It is interesting to note that the light stimulus, contrary to expectation, did not predominate over gravity. An increase of the light intensity from 16 candle power to 40 made no difference in the results.

A set of records from an experiment in which the light was below the cylinder and therefore acted contrary to gravity is given in Table III.

TABLE III

Showing the position of 5 flies in 14 trials after having been in the light box with a single lamp (15-watt Mazda) below the cylinder; 55.7 per cent crept to the uppermost third.

NUMBER O	DE FLIES	IN THE	DIFFERENT	SECTIONS	OF CYLINDER

Trial number.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	Total
Section 1	2	2	3	2	1	2	1	3	2	4	2	2	2	1	29
Section 2	1	1							3	1	2	1		1	10
Section 3		1	1	2		1		,			1				6
Section 4					2	1	1							1	5
Section 5,	1	1		,	1		1	1					2	1	8
Section 6	1		1	1	1	1	2	1				2	1	1	12

These results corroborate previous work on this subject in so far as a negative response to gravity is concerned. But in this, as well as in all previous work, mechanical or light stimuli have been operating. The former cannot be eliminated in such experiments since it is impossible to invert the cylinder without moving it. Consequently I next tried a series of centrifuging experiments in which these two kinds of stimuli could be neglected. So far as I am aware the effect of centrifugal force on Drosophila has never before been studied.

4. Effect of centrifugation.—The centrifuge consisted of a table mounted on a base capable of revolving, on a fixed axis in a horizontal plane. A small water motor attached to an ordinary faucet furnished the motive power. On the table could be fastened glass tubes of various lengths and bores. In these tubes, the ends of which were tightly corked, one or more flies were placed in the desired position; the tube was then revolved about its middle point as a center at a known speed, the time of revolution usually being one minute.

In the preliminary trials it was found that at a certain speed the flies in the ends of the tube crept toward the center and remained there. If the speed was greatly increased, they were thrown out to the ends. It became necessary therefore to determine the maximum and minimum limits within which a definite response could be noted. The calculation was made according to the formula, $F = \frac{mv^2}{r}$, where F represents the

centrifugal force, m the mass, v the velocity of revolution and r the radius. Experiments showed that when F was equivalent to gravity the flies began creeping toward the center. When it was considerably larger than gravity the flies were thrown out to the ends. Furthermore when F was just equivalent to gravity the flies crept toward the center until they reached a point where the force was less than gravity, the speed remaining the same. To induce further creeping toward the center the speed had to be increased, since the shorter the radius of revolution the greater the speed necessary to generate the same force.

The tube ordinarily used was 50 cm. long with a diameter of 2 cm. Applying the formula, $n = \frac{980}{4\pi^2 r}$, which can be de-

rived from the previous one, the speed necessary to generate a force equivalent to gravity is easily calculated. When the flies are in the ends of the tube, therefore, it must revolve approximately once every second; as they move toward the center the speed must be gradually increased. But since the flies can creep against a force much greater than gravity without losing their equilibrium, a constant speed can be found at which they will creep all the way to the center. This is about 85 revolutions per minute. Experiments carried out in darkness, in dif-

fuse daylight, and with a bright light at one side all gave similar results. A check experiment, in which the speed of revolution was very low (from 1 to 40), showed the flies creeping about indifferently; therefore it was concluded that mechanical and light stimuli did not affect the response in these experiments.

One hundred trials with 40 different animals, under the various conditions described above, showed that a speed of 60 revolutions per minute was necessary to start them moving toward the center. As the flies approached the center the speed had to be gradually increased in order to keep them moving toward the center. At a distance of 2 cm. from the center a speed of approximately 210 revolutions per minute was necessary to accomplish this. At a distance of 25 cm. from the center any speed greater than 100 revolutions per minute mechanically prevented the flies from creeping toward the center. Table IV gives the data for several trials taken at random from the series of 100.

TABLE IV
Showing the position of 14 flies in 8 trials after one minute of revolution at different speeds.

Number of flies	Position at beginning	Number revolutions per min.	Time of revolution	Position at end of experiment
2	End	50	1 min.	End
2	End	72	1 min.	½ way from end
1	End	90	1 min.	Center
1	3 way from end	120	1 min.	End
2	½ way from end	72	1 min.	3 way from end
2	½ way from end	96	1 min.	Center
3	End	100	1 min.	End
1	2 cm. from center	210	1 min.	End

These experiments demonstrate a very definite response and prove that Drosophila reacts negatively to a centrifugal force equal to or slightly greater than gravity, as well as to a gravitational one, without regard to other stimuli. We may therefore consider gravity a kinetic stimulus as well as a directive one.

5. Effect of air currents.—The next question considered was, How does Drosophila respond to air currents? Horizontal, upward, and downward currents, produced by an electric fan, were directed into a glass cylinder like the one used in the dark box. Their strengths were so adjusted that the flies did not lose their equilibrium.

(a) Horizontal currents.—These trials, carried out in diffuse daylight, did not give as definite a response as could be desired. The flies were liberated singly from the bottle containers at the open end of the cylinder, and their course of locomotion noted. In only 11 trials out of the 40 made, could the response be called definite. In 7 of these the flies crept against the current, in 2 they crept against it for about 10 cm. and then flew with it, and in the other 2 they flew with the current. Every case of creeping was against the current and every case of flying was with the current. In the control experiments with no air currents the flies crept or flew in any direction.

(b) Upward vertical current.—In these trials 29.5 per cent of the flies crept upward with the current, 59 per cent flew upward, and 11.5 per cent crept downward. Gravity is here acting contrary to the force of the current and the 29.5 per cent creeping up is probably a purely negative geotropic response. The creeping downward was very slow and intermittent. The largest

number (59 per cent) flew with the current.

(c) Downward vertical current.—The results of 61 trials showed that 27.8 per cent of the flies crept upward against the current, 23.2 per cent flew upward, while 49 per cent flew downward with the current. An interesting observation was that practically all the flies crept upward a short distance before carrying out the main response. In the control experiments, with no air current and the cylinder in a vertical position, the only reaction that could be noted was a negative geotropic one, the other movements being indifferent.

There is therefore a tendency for Drosophila to fly with the air current, a positive response, and to creep against the current, a negative response. Since there were extremely few flying responses in the experiments with gravity and centrifugal force, no comparisons can be made with them. But the creeping against the currents corresponds with the negative response to

gravity and centrifugation.

DISCUSSION

The responses, other than mechanical ones, of animals to centrifugal force and air currents have not been thoroughly investigated. Only a few references to centrifuging experiments are found in the literature. Loeb ('91) stated that Cucumaria cucumis responds to centrifugation by contracting its body and remaining motionless. This condition persists for from one-quarter to one-half an hour afterward, when crawling is begun again. Although he studied the geotropic reactions of certain caterpillars, ephemerid larvae, coccinellids and blattids, no reference is made to testing the effect of centrifugal force on them.

Jensen ('93), having found that Paramoecium was negatively geotropic, discovered that it moved centripetally with weak centrifugation. Davenport and Perkins ('97), after concluding that "gravity acts as an irritant to which the organism makes a response, belonging to the category of adaptive responses," say that this irritating pressure "may be replaced by a centrifugal pressure, when the same geotactic orientation will occur." Harper ('11) also reported that Paramoecium reacted negatively with weak centrifugation. He believes, however, that "the response of Paramoecium to gravity is a purely mechanical tropism."

On the other hand, geotropism of animals has been extensively studied, and many theories put forth for its explanation. It is generally accepted that the ear or some "static" organ controls this tropism in certain forms. But for insects there is much doubt as to how the stimulus is received. Kafka ('14) reviews this question and summarizes the different theories, as follows: Loeb believes that the chordotonal organs at the base of the halteres of some Diptera are the organs of reception. Pflügstaedt and Weinland describe other structures which might serve as sense organs. Similar organs have been described by Hochreuther for Dytiscus, by Janet for Hymenoptera, and by Baunacke for nepid larvae. But conclusive proof that any of these organs, the functions of which are little understood, control the response to gravity is entirely lacking.

The reactions to the three kinds of forces described above suggest an explanation as to how the stimuli are received. When the fly is creeping upward against gravity the weight of the body is on the legs. There is, therefore, a tension on the leg muscles distinct from that caused by creeping. When a fly is creeping against centrifugal force a similar tension of the leg muscles is produced. Furthermore, creeping against an air current causes the same kind of tension. Very probably, then, the stimuli in all three cases are due to this tension and are received by the sensory nerves of the leg muscles, the response being an attempt to preserve the equilibrium of the body. Negative geotropism in Drosophila, then, is concerned with the muscle sense. Radl ('05) expressed the view that the insect muscles are capable of acting as special sense organs when he wrote "das Gehör der Insekten ist ein verfeinertes Muskelgefühl."

The flying response does not fit into this explanation and it may be that it is not influenced at all by gravity. It is a matter of common observation that the house flies on a brightly illuminated window usually creep upward but fly in all directions. The flying is much more indefinite than the creeping. In my observations on geotropism only a very few cases of flying (about 3 per cent) were seen. Cylinders with a diameter as large as 12 cm. were used so as to allow flying, but no greater proportion of cases was seen than in the smaller cylinders. When disturbed the animals flew about indifferently for a short time and then, after alighting, continued their upward creeping. In the centrifuging experiments no flying at all was seen. The air currents often caused flying, and in the large percentage of cases the animals flew with the current, although they were able to withstand it. It seems therefore that the response to gravity is much less marked in flying than in creeping, where it is very definite.

CONCLUSIONS

1. Drosophila ampelophila Loew, when creeping, reacts negatively to gravity, to a centrifugal force which is equal to or slightly greater than gravity, and to air currents without regard to other stimuli. Gravity is, then, a kinetic as well as a directive stimulus.

2. The stimuli causing these reactions are probably received by the sensory nerves of the leg muscles.

3. It is probable that flying reactions of Drosophila are not influenced by gravity.

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GEOTROPISM IN PLANARIA MACULATA

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Flat-worms, such as planarians, are commonly collected from the *underside* of stones in a stream or pond (Bardeen, '01; Pearl, '03; Whitehouse, '14). The resting position of these animals, with their ventral surfaces uppermost, would seem to indicate a negative response to gravity, since when moving they may be in any position, depending upon the particular surface over which they happen to be gliding. This investigation has as its object the analysis of the resting behavior of these worms. The specimens used were Planaria maculata Leidy and were taken from Fresh Pond, Cambridge, Mass. A stock was brought into the laboratory and kept in a large jar on a table about four feet from a north window.

To ascertain the relative importance of light and gravity in the reactions to be studied, an experiment in the following form was carried out. One-half of one surface of a glass plate, 10 x 8 cm., was coated with black wax. This plate was supported in a horizontal position by wax feet 4 mm. high on a second glass plate. The pair were placed in a flat dish and covered with water to the depth of 3 cm. The flat dish had a collar of black paper about its sides, so that only light from above could fall on the plates. Then twenty planarians were placed at one time on the upper plate, at another on the lower one, and their positions recorded twice a day. As the animals moved about over the whole dish for an hour or more after beginning the experiment, the fact that they had started from the upper or lower plate was not significant.

The results of 30 readings showed that 30 per cent were not under the plates, but usually in the shadow near the angle between the bottom and side of the dish, 70 per cent being

found between the plates, and always under the black half. Of the latter, one-fifth were on the under side of the upper plate (ventral surface up), and four-fifths on the lower plate (dorsal

surface up).

Since, as the preceding experiment showed, the influence of light was so marked, it was decided to eliminate this factor by conducting all the subsequent experiments in a light-proof box. To eliminate thigmotropism and to provide a continuous surface which should have all possible relations to gravity, spherical balloon flasks were used. These flasks were 13 cm. in diameter. They had a short neck 4 cm. long. Three regions of equal area were marked off on the surface of each flask, a ring about its equator and a segment at either pole. These three regions were designated top, middle, and bottom. The flasks were so marked that in one the neck came in the top, in another in the middle, etc. In the experiments very few worms lodged in the neck and the per cent of such was practically the same whether it occurred in flasks with the neck in the top area, in the middle, or in the bottom. In the tabulation of results worms in the neck are not included.

Twenty worms were used in each experiment. Readings of their positions were made at 9 A. M., 1. P. M. and 4. 30 P. M. In a few cases readings were taken at intervals of two hours, but even then the animals were at rest. They were made to start moving before being returned to the box, as a means of redistributing them for the beginning of another trial. It was found that the positions of the planarians in the flasks changed greatly during the first few days after being put into the dark. At first the majority were to be found in the bottom of the flasks. A few days later they were equally distributed in the three areas. When they were fed there was a sudden departure from this equal distribution and the majority would be found in the top. They again distributed themselves equally in the three areas three or four days after feeding. Table I gives a summary of results. The numbers are the per cents taken from 10 or more readings. By "from light" is meant worms taken from the stock which had been kept in the light. "From dark" means worms which had been in the dark-box for a week or longer. "Fed" worms are those which were fed on liver on the day of the experiment or every other day

during experimentation. "Unfed" are those which had been without food for five days or more.

From these results it is evident that two factors are concerned in the distribution of the worms: First, previous history as regards exposure to light, and second, the state of metabolism of the worms in relation to feeding. Both fed and unfed worms which had previously been in the light were found to be mostly positively geotropic immediately after being put in the dark. The fed ones then became negative for a short time. Finally both became indifferent if feeding was stopped. Those which had been in the dark for a long time were negative when fed and indifferent when unfed. Walter ('08) makes the statement that Planaria gonocephala "seems, after several hours of exposure to the dark, to be positively geotropic," while Kafka ('14, p. 151) says that Planaria gonocephala is negatively geotropic after long retention in the dark. Both of these apparently contradictory statements are probably true, since the length of exposure to the dark may very well be an important factor in the geotropism of Planaria gonocephala, as my experiments show for its close relative, P. maculata.

That this negative geotropism of fed worms in the dark is not in reality a response to oxygen from the open neck is shown by the following experiment. A flask containing 20 planarians was completely filled with water, and the mouth covered by a glass plate. It was then immersed neck downwards in a jar of water in the dark-box. Previous to the experiment the planarians had been fed every other day for two weeks, and were dividing so that at the end of the experiment there were 27 worms instead of 20. The per cents found in the three areas of the flask under these conditions were as follows: Top, 58; middle, 33; and bottom, 9. These are of the same order as the last two series of the per cents given in Table I. Table II shows this relationship.

TABLE I

			Are	Area of the Flask		
			Тор	Middle	Bottom	Month
		1st 2 days in box	19	10	71	Nov.
	Unfed	1st 2 days in box	17	21	62	Jan.
		5+days in box	38	24	38	NovJan.
From light	Fed before expt.	1st 2 days in box	16	21	63	Nov.
		3rd, 4th days in box.	63	21	16	Nov.
		5th day onward	` 36	. 23	41	Nov.
			36	30	34	Nov.
	Unfed		38	35	27	Dec.
From dark			35	36	29	Jan.
From dark	Fed contin-		58	28	14 .	Dec.
	uously		68	26	6	Jan.

TABLE II

		A	rea of Fla	sk	Month	
		Тор	Middle	Bottom		
	Flask open to air	58	28	14	Dec.	
From dark and fed	riask open to an	68	26	6	Jan.	
and icu	Flask submerged in water	58	33	9	Jan.	

Table II shows that the per cents were the same whether the flasks were open to the air or entirely submerged in water. If the worms had been responding to oxygen and not to gravity, we should expect in this experiment to have found them in the bottom near the mouth, where oxygenated water could enter from the jar outside. They were actually found in the region

farthest from the supply of oxygen, so that their position was a true response to gravity.

To find whether the presence of the slime tracks influenced this behavior, indifferent animals were kept for a week (1) with no change of water, but the slime washed out from the flask daily, (2) with change of water daily, but the slime not washed out, and (3) with no change of water and no cleansing of the flask. Table III gives a summary of results.

TABLE III

		A	rea of Fla	sk
		Тор	Middle	Bottom
	Slime washed out daily	44	30	26
Unfed and from dark.	Water changed daily	29	31	40
	No washing or change of water	35	26	29

Since the planarians remained practically as indifferent to gravity throughout the experiment as they were before it was begun, the presence or absence of slime tracks probably had little effect on their geotropism.

The results of these experiments are in line with observations on the stock animals. They usually remain in the shadow under the stones and along the side of the dish. The majority rest on the underside of the stones, but a great many are to be found on the sides of the dish. Immediately after they finish feeding, they glide to the top and move about over the dish. If the water is changed at this time they soon come to rest near the bottom again. If the water is allowed to get foul after feeding, they remain at the top, probably in this case on account of lack of oxygen below. I have been unable to see daily migration such as Walter ('08) observed.

It would seem reasonable, therefore, to suppose that the collector who finds planarians ventral surface up on the underside of rocks, sees those which have been feeding, while if he looked in other places he might find the unfed ones in any position.

Since Planaria maculata has no otocyst, it may be that after eating, the food in the digestive tract serves as an otolith, and after digestion and assimilation the animal becomes indifferent to gravity because the food is no longer able to press upon the digestive epithelium. This does not account for the fact that fed worms are positively geotropic when first put in the dark.

I wish to thank Dr. Parker for suggesting the problem and for advice as to methods.

CONCLUSIONS

1. Unfed Planaria maculata which have been in the light are positively geotropic when first placed in the dark. After several days in the dark they become indifferent to gravity.

2. Fed Planaria maculata which have been kept in the light are likewise positively geotropic at first. But they become negative after two days and indifferent after five days.

3. Fed planarians which have been in the dark for some time are negatively geotropic.

4. The presence or absence of slime tracks has no influence on the geotropism of these planarians.

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